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HERPETOFAUNA OF THE SOUTHEASTERN HIGHLANDS OF GUATEMALA*

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INTRODUCTION

LYING east of Guatemala City and south of the Río Motagua is a section of Guatemala that is known locally as the *oriente*. Though some of this terrain more properly belongs to the Pacific coastal plain and other parts are to be included in the Caribbean lowlands, the greater part of the region is a plateau averaging some 1000 m. elevation and surmounted by higher blocks and volcanos that attain a maximum height of about 2500 m. More exactly delimited, the Las Vacas Valley, in which Guatemala City is situated, marks the western boundary of these uplands.

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To the east and southeast the Honduran and Salvadoran borders delimit their extent. To the north the 500 m. contour on the south side of the valley of the Río Motagua (Map 1) and its headwater streams serves as a generalized boundary. On the south a line drawn so as to connect the crests of the volcanos Pacaya, Tecuamburro, Cerro Quemado, and Moyuta, with the exception of some low-lying valleys that invade the uplands, serves as a suitable limit. To this region I apply the name Southeastern Highlands in contrast to the higher Southwestern Highlands to the north and west of Guatemala City.

Included within these limits are some 10,000 sq. km. of terrain. This region by itself does not constitute a natural area. Geologically, it is merely the northern and western end of the general upland mass that extends southward to southern Nicaragua and biologically it may have a similar extent. Certainly, the herpetofauna of the Southeastern Highlands is very like that of parts of upland El Salvador and what little is known of upland Honduras to at least the Honduran Depression.

Though settled since the earliest colonial times, relatively easy of access, and with a population that is predominantly European and both courteous and friendly, this region is biologically one of the least known parts of Guatemala. It remained almost unheeded by the English naturalists Godman and Salvin and their collectors; the American ornithologist Anthony, who collected in practically every other part of Guatemala, neglected it; and even the indefatigable Karl Sapper paid it only a passing visit. Not until very recently have any biologists explored it (Saunders, Holloway, and Handley, 1950, and Tashian, 1953), and herpetologically it was, until my own investigations in 1952, known from only a handful of specimens.

My main reason for undertaking an exploration of this region was to obtain some general information concerning its herpetofauna, a need that I have experienced for some time in connection with my studies on the amphibians and reptiles of Cuatemala. Furthermore, as knowledge of middle Central America has increased, some interesting geographic anomalies in the herpetofauna have become apparent, and the key to the explanation of these seemed to lie in this general region. Finally, since little is known of the moderately elevated uplands of middle Central America that stand out in striking contrast to very high plateaus farther north, it was believed that information concerning the southeast might prove of some value to interpretation of such data as might be forthcoming from similar regions to the south.

Accordingly, accompanied by Mr. Luis de la Torre, who was delegated to collect mammals for the Chicago Natural History Museum, I proceeded to southeastern Guatemala in January, 1952. It was decided that we would devote the greater part of our time to a study of the faunas of three major regions. In the east, near the Honduran border we chose Esquipulas which, at 950 m., seemed to offer conditions that might be typical of those over most of the uplands of the southeast. Here, too, we would encounter whatever species invade the plateau from the Caribbean lowlands. In the north we selected Jalapa, somewhat higher than Esquipulas but still within reach of the general upland surface, and from where we could reach the highest elevations in the southeast. And third, we chose Jutiapa in the southwestern portions of the Southeastern Highlands, where we would be in proximity to the lowest elevations in the southeast, and, in addition to the plateau surface at elevations comparable to those at Esquipulas, we would be able to study entrants from the Pacific lowlands. Though Mr. de la Torre was unable to accompany me after May, my studies in the region extended from February until early July. Owing to numerous interruptions only about one-half of that time was actually spent in the field in the southeast.

The results of these investigations with such material as I had secured during brief visits to the region in both 1944 and 1949 revealed that a disappointingly small herpetofauna inhabits the region. Less than 1300 specimens from all sources have been available. These are divided among 59 forms (species and subspecies). Though the collections from the region are sparse both in individuals and species, I believe that sufficient data are available to permit a few suggestions concerning the problems previously inferred.

In the following account I have not hesitated to make use of unpublished data secured during the course of my studies on the Pacific versant in 1947, 1949, and 1952 and on the Motagua Valley in 1952. A report on the former is now being prepared.

Acknowledgments

In assembling and studying the data set forth in the following I have received aid and advice from a number of individuals and institutions. To these I take this opportunity to express my gratitude. For the privilege of utilizing materials under their charge and for their advice and aid I am indebted to my colleagues at the University of Michigan, Dr. Charles Walker and Dr. Norman Hartweg. For arranging loans of specimens contained in their respective museums I wish to thank Mr. Charles Bogert of the American Museum of Natural History, Dr. Doris Cochran of the United States National Museum, Dr. Edward Taylor of the University of Kansas, and Mr. Clifford Pope of the Chicago Natural History Museum.

For the courtesy and hospitality which they extended to me during the course of my field studies I am grateful to Mr. and Mrs. Reginald Odonnell of Granja Los Ocales, Señora Trinidad Alarcón of Hacienda Mongoy, and Señor Manuel Cruz, administrator of Aserradero San Lorenzo. To Señor Jorge Ibarra, director of the Museo Nacional de Historia Natural in Guatemala, I am especially indebted for his tremendous aid in securing me permits and special privileges from his government.

Mr. William Brudon, staff artist in the Museum of Zoology, has been most generous with his aid and advice relative to drafting and photographic problems.

Finally to my co-worker in the field, Mr. Luis de la Torre, I wish to extend my thanks for his aid and congenial companionship.

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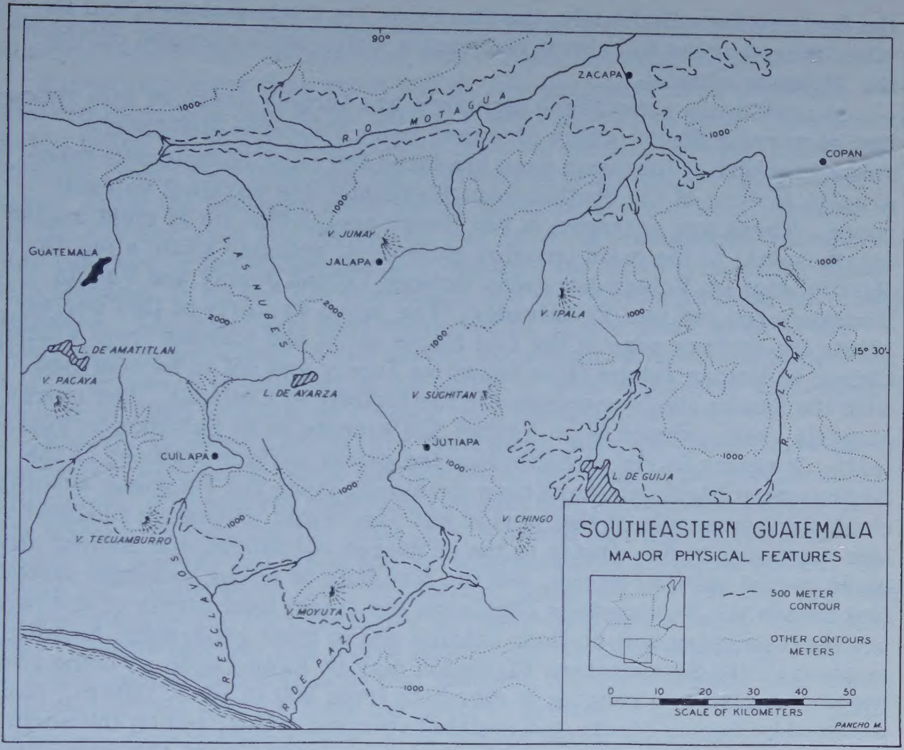
DESCRIPTION OF THE SOUTHEASTERN HIGHLANDS

From the standpoint of physical geography the Southeastern Highlands have been so poorly explored and so infrequently considered in the literature that a description of the region is extremely difficult. What little is known of the geology and physiography of the area is given in the works of Sapper (1894, 1899, and 1937), the earlier two studies having been summarized by Schuchert (1935), and such observations as I was able to make are added on the following pages. Concerning the climatology even less is known. From within the Southeastern Highlands proper climatological data on but three stations are available. These, Ipala, Agua Blanca, and Anguiatú in the basin of Lago de Güija, all are along the railroad between Zacapa and San Salvador. For them but a single year's temperature (date unknown) and seven years' (1941-47) rainfall are recorded. A few other stations along the southern edge of the highlands and a few notes in Sapper (1932) provide the remainder of what little data are useful. Recent annual reports from the Observatório Nacional de Guatemala give evidence that this situation is now being remedied. For notes on vegetation the writings and maps of Sapper (1894), Standley and Steyermark (1943), and Steyermark (1950), all of which are in remarkable accord, permit some generalizations. Our knowledge of the physical geography of the Southeastern Highlands is drawn almost entirely from the above references.

Geology and Physiography

Of the 10,000 sq. km. included within the limits of the Southeastern Highlands, 50 per cent lies above the 1000 m. contour (for physical features, see Map I) and the remainder does not descend below the 500 m. contour. Not more than 2 per cent ascends above 2000 m. and the highest point lies on the ridge between Mataquescuintla and Jalapa near the little settlement of Miramundo, where the elevation is near 2600 m. Though this area comprises a natural region within the limits of Guatemala, it should be noted that it extends extralimitally into Honduras and northern El Salvador at least to the Honduran Depression. This entire unit stands in striking contrast to the Southwestern Highlands of Guatemala (see Stuart, 1951) to the west, which do not descend below 1500 m. and for the most part lie above 2000 m., with a maximum elevation of about 3600 m. In other words, the Southeastern Highlands begin where the Southwestern Highlands end.



MAP 1

Though it is believed that the region, like all Nuclear Central America, has been a positive element since at least Paleozoic times, the young adesites and basalts (very probably of Pliocene and post-Pliocene origin) that now mantle the Southeastern Highlands render positive proof of this hypothesis difficult. Two main entities appear to have formed the backbone of the Southeastern Highlands. To the west and south the Las Nubes block (roughly between the levels of Guatemala City and of Jalapa) may be a continuation of the main mountain backbone of the Southwestern Highlands. Lying to the north of this and bordering the Motagua Valley on the south are the remnants of an ancient mountain axis that roughly parallels the Sierra de las Minas (to the north of the Motagua Valley) and which continues into Honduras as the Sierra de Espíritu Santo, which with its associated ranges is known by a number of local names. Both of these masses, and especially the Sierra de Espíritu Santo, have now been so thoroughly eroded that their main west-east axes are barely discernible. Las Nubes, which attains the highest elevations in the Southeastern Highlands, appears to be much the younger and is apparently comparable to the blocks that form the Sierra Madre, the Southwestern Highlands, the Sierra de los Cuchumatanes, and the other upland areas in central Guatemala which were elevated during the Pliocene orogeny.

As previously noted these highlands are largely overlain with andesites of varying depths which stemmed from Pliocene-Pleistocene volcanism that at the same time produced the most conspicuous topographic feature of the Southeastern Highlands, the dormant volcanic cones. These are arranged in two linear series that lie at right angles (north-south) to the main (roughly east-west) volcanic chain along the Pacific, that is, Volcán Lacandón through Volcán Jumay and Volcán Tecuamburro and into El Salvador. The more westerly of this series skirts the eastern edge of the Las Nubes block and extends from Volcán Chingo to Volcán Jalapa (also known as Jumay and not to be confused with the Jumay above mentioned in the vicinity of Cuilapa). The more easterly chain extends from Volcán San Vicente in El Salvador to Volcán Ipala. It seems fairly probable that the extant surface features of the Southeastern Highlands have been developed since the Pliocene, when the orogenic movements of that period and associated volcanism initiated a new erosional cycle. Owing to the scattered volcanism, the ancient and more recent uplifted blocks, and the diversity of minor drainage systems that invade the Southeastern Highlands the extant land-forms of the region are most complex both in their origins and in their geographic mosaic. In general, the Southeastern Highlands may be looked upon as being composed of a platform ranging in elevation from 800 to about 1200 m., surmounted by higher blocks and isolated volcanic cones, and on the north descending to the Caribbean lowlands (more properly the Motagua Valley) and on the south to the Pacific coastal plain in a sharp escarpment. I have noted previously that to the west they merge with the higher Southwestern Highlands and to the east with the uplands of Honduras and El Salvador.

The basic platform occupies most of the southern and eastern sections of the area. In general at elevations of 800-1200 m. the landscape is one of plains and rolling uplands (Pl. II, Fig. 1). In places, such as along the railroad between Ipala and the descent into the Güija Basin, the upland surface is remarkably level, and even as the edge of the southern escarpment is approached, as in the vicinity of Jutiapa, the local relief is not great. Above this level are the scattered volcanic cones (Pl. I, Fig. I) which rise to elevations not exceeding 2150 m. (Volcán Jalapa or Jumay), and which are so numerous that at least one is almost always visible in the southeast. Such elevations are very local, and except for the rugged *pedregal* that may surround their bases (Volcán Suchitán and Volcán Ipala especially) their influence on the adjacent highland surface from which they rise abruptly is negligible. The smaller streams that cross this upland surface are generally contained in steep-sided small barrancas that have been cut in the ash cover that mantles most of the region. Not until one approaches the edges of the plateau do such streams have much velocity, and some are almost sluggish. Some of the larger streams in contrast, e.g., the Río Ostúa that feeds Lago de Güija and which may lie in a structural valley, have slashed canyon-like valleys back into the level plateau surface.

Elevations lower than about 800 m. are encountered on the Southeastern Highlands only in the larger river valleys and along escarpments. In the latter the relief is extremely high, as smaller streams converge to form rivers that flow onto the lowlands through deep, V-shaped valleys. Along the southern escarpment the tributaries of such streams as the Río Esclavos and the Río de Paz have cut tremendous barrancas into the edge of the upland surface, while to the north tributaries of the Río Motagua, e.g., the Río Chimalapa and the Río Chiquimula, have done likewise. The only level land below 900 m. is one small area on the Southeastern Highlands in and around the village of Asunción Mita (Pl. I, Fig. 2), which is situated on the plains of what apparently was formerly an arm of Lago de Güija or a small lake connected with it.

Elevations above 1200 m. are restricted, with the exception of the volcanic cones, to the north and northwest portions of the Southeastern Highlands. The ancient mountain remnant that borders the region on the north presents, for the most part, subdued features on the side facing the plateau and gives one the impression of a rolling upland. Its steep and rugged north face, in contrast, drops off sharply into the valley of the Motagua and its tributaries and is broken by numerous barrancas. The recently uplifted Las Nubes and Soledad Grande blocks (probably a single geomorphologic unit) that make up the northwestern quarter of the region rise sharply from the general surface of the plateau. Small streams, mostly intermittent, have carved short, steep barrancas in their sides, but once the high crest is attained, one encounters a rolling, high-level surface of only moderate relief (Pl. IV, Fig. 2.).

Some of the most rugged terrain on the Southeastern Highlands is in the eastern part of the region. Here the ancient mountains noted above merge with the complex ranges along the crest of which runs a considerable portion of the Guatemalan-Honduran border (Pl. I, Fig. 1). Though these mountains are much lower than those in the west, local relief is considerably greater. Here the drainage pattern becomes confused, and one's general impression of the region is that of an unoriented jumble of mountains within which are nestled alluvial basins of which that of Esquipulas is the largest.

Hydrographically, the Southeastern Highlands are not particularly complex. The Continental Divide, which is extremely irregular and somewhat closer to their northern than to their southern boundary, crosses them along an east-west axis. Inasmuch as rainfall does not exceed about 1200 mm. over most of the region and since the dry season is long and severe, the flow of streams and the volumes of the few lakes in the region are in general neither large nor regular. Only one lake of any size occurs on the Southeastern Highlands, Laguna de Ayarza, a crater lake of some 28 sq. km. surface and a maximum depth of 229 m. (Holloway in Saunders *et al.*, 1950: 109). Atescatempa near the Salvadoran border is only one-tenth the size of Ayarza and fluctuates between half to double that size. Smaller "puddles" are scattered here and there over the highlands. One of the most interesting of these is Laguna Retana, which occupies a structural depression on the north side of Volcán Suchitán. Today it is almost dry and though famous for water birds that congregate there at certain seasons of the year, the greater part of the basin is under cultivation.

No stream of any size is found on the plateau proper. The majority of the brooks are shallow and, as noted previously, are contained for the most part in steep-walled barrancas. During the time of local rains they may carry a considerable volume, but often during the dry season they may be reduced to mere trickles or go completely dry. Only where the smaller streams join near the edges of the highlands to descend to the lowlands of adjacent areas do large streams of considerable volume and velocity occur.

Three major drainage systems may be recognized. The greatest volume of water is carried from the Southeastern Highlands by streams that descend the southern escarpment, cross the Pacific coastal plain, and empty into the Pacific. The Río de los Esclavos and the Río de Paz are the largest of these. The northern part of the highlands drains either directly into the Río Motagua (and thence to the Caribbean) or into its tributaries through such streams as the Chimalapa and the Zacapa. A third drainage system carries waters arising in a narrow strip of the region along the Honduran and Salvadoran borders. Streams in this area are the headwaters of the Río Lempa that crosses El Salvador, or they feed Lago de Güija which in turn empties into the Lempa.

Climate

Owing to the inland position of the Southeastern Highlands with their latitudinal extent of but 30′ and to their subhumid conditions, they are subjected to temperature variations that are essentially a function of altitude. In the single year for which temperature records exist the annual means of Ipala (820 m.) and Agua Blanca (890 m.) were 22.0° and 22.4°, respectively. These means are in accord with those of comparable Guatemalan stations for which more extensive records are available. Annual variation in monthly means probably amounts to less than 6° between the warmest and coldest months. Thus, it is probable that at roughly 900 m. elevation on these highlands the coldest month (probably January) has a mean of about 19° and the warmest (probably May) of about 25°. If a normal temperature reduction with increasing altitude (0.6° per 100 m.) is assumed, all of the Southeastern Highlands below an elevation of roughly 1000 m. lie within the *A* (frost free) temperature belt of Köppen (1923). With elevations not in excess of about 2600 m. the remainder of the Southeastern Highlands lie within the *C* (occasional frosts) temperature belt of Köppen. At elevations above ca. 2000 m. the extremes and variations in temperature are probably modified somewhat by the greater amount of atmospheric moisture. Nevertheless, hail is not unknown at higher levels within the region.

Though distinctly subhumid, the Southeastern Highlands lie on the mesic side of the *B* boundary of Köppen. Ipala receives 780 mm. of rainfall annually and Agua Blanca 750 mm. Between 85 and 90 per cent of this precipitation is concentrated in the high-sun period. These two stations, situated in the eastern part of the region, probably receive as little rainfall as any part of the Southeastern Highlands. To the south and southwest precipitation increases notably. Along the rim of the Southeastern Highlands above the slopes of the Pacific versant the mean annual rainfall at several stations at 700 m. elevation between Cuilapa and Jutiapa amounts to between 1500 and 1600 mm., and at Cerro Redondo (1200 m.) the average annual rainfall is in the neighborhood of 1900 mm.

The lower temperatures at higher elevations greatly increase the relative humidity of the air masses of low absolute humidity over the Southeastern Highlands. At about 2000 m. elevation a somewhat sharp break in moisture conditions occurs. Though actual rainfall above that level may not be greatly increased, atmospheric moisture produces far more mesic conditions than are found at lower elevations. Thus, at Soledad Grande (2500 m.) heavy night dews are the rule even at the height of the dry season. These dews are sufficient to permit the planting of corn in the region some two months before it is planted at lower elevations, and on March 17 there were fields in which it stood ankle high. The broadleaf forest of that region as well as that on the crest of Volcán Jalapa (lower limit, 2000 m.) was wet and dripping during the dry season, and the mulch on the forest floor was soggy in the extreme. While in the Jalapa region I do not recall a morning when the crest of that volcano was not shrouded with mist. This atmospheric moisture in conjunction with reduction in evaporation that accompanies reduction in air temperatures produces at these higher elevations the most mesic conditions encountered on the Southeastern Highlands.

It is impossible to say whether the Caribbean or the Pacific is the main source of the precipitation of the region. The Motagua Valley, up which the prevailing Northeast Trades could flow, would seem to suggest the Caribbean as the main source. However, the remnants of the ancient mountain arc that borders the Southeastern Highlands on the north could conceivably act as a barrier to winds from the Caribbean. Rainfall curves for both Ipala and Agua Blanca are very similar to those of stations in the Motagua Valley, while curves for stations in the west and south are more typical of those of the Pacific coast. Anguiatú (500 m.) in the Güija Depression and lying below the general upland level to the north has a rainfall curve that suggests that precipitation may be derived from both the Pacific and Caribbean. It is noteworthy, furthermore, that inhabitants of the Jalapa region in the north central part of the Southeastern Highlands look to the south (and hence to the Pacific) for their rains. It is not improbable that the prevailing winds from the northeast, together with local winds from the Pacific and irregular impacts of hurricanes that develop in the Caribbean during the high-sun period all contribute to the rainfall of the region. Certainly, the pressure belts and accompanying moisture-bearing winds that cross the low uplands of southeastern Guatemala and of Honduras must present a most complex pattern.

It is suggested that in the Köppen system all terrain on the Southeastern Highlands lying below 1000-1100 m. may be classified as *Aw* while that of higher elevations is unquestionably *Cw*.

Most important to an understanding of the extant distribution of many species of amphibians and reptiles is a knowledge of paleoclimates, especially those of the Pleistocene. Unfortunately, no data have been forthcoming on the past climates of Guatemala. One may, however, draw certain inferences concerning the climates of the recent past.

With reference to temperature there can be little doubt that the extant temperature belts were at very much lower elevations during the period of maximum Pleistocene refrigeration, but I have previously given reasons for believing that at no time was the environment at sea level in Guatemala such that, as suggested by Griscom (1932: 63), a subtropical fauna could survive at very low elevations (Stuart, 1951: 28-29). In fact, insofar as the subtropical herpetofauna of Guatemala is concerned, those extant species the vertical limits of which are controlled by temperature, and hence altitude in this small country, would require a reduction of about 9^0 in temperature to find suitable environments at sea level. Flint (1947: 455-56) suggested a maximum temperature reduction of no more than 8^0 over most of the globe at the height of refrigeration. Certainly, a reduction of no more than 6^0 would permit most of the forms characteristic of the higher elevations of the Southwestern Highlands to invade much of the Southeastern Highlands and as little as 1.5^0 reduction would permit some species, e.g., *Plectrohyla guatemalensis* or *Hypopachus barberi*, to survive throughout the Southeastern Highlands. In my opinion a reduction of no more than 5^0 would be ample to explain the distribution of the majority of highland Chiapan and Guatemalan species on isolated peaks of the Southeastern Highlands and adjacent Honduras and El Salvador. Such a temperature would even permit the assumption of considerable uplift in those regions during relatively recent times.

With regard to rainfall, I believe that there can be little question but that the Southeastern Highlands have at various times during the Pleistocene been considerably more humid than at present. The now almost dry Laguna Retana gives evidence of having, in the not too distant past, filled its large structural basin. The plains in the vicinity of Monjas are suggestive of lacustrine origin, and I do not doubt that a competent physiographer (if such is to be found) would agree that Lago de Güija is a remnant that formerly probably extended into the Asunción Mita region, the plains of which are lacustrine. Further, many of the barrancas that cut back into the Southeastern Highlands suggest that they were carved by streams of considerably greater volume than is now carried in them. Beyond these extrapolations and suggestive physiographic features there is no evidence as to the exact nature of the climate of the Southeastern Highlands during the recent past, yet the conclusions set forth above are certainly born out by zoogeographic patterns.

Vegetation

As a generalization three major vegetational belts may be recognized on the Southeastern Highlands. At elevations below 1000 m. on the average both Standley and Steyermark and Steyermark indicate the occurrence of "desert-chaparral" and their limits of the cover are essentially the same as those of the "grass and shrub steppe and chaparral" of Sapper. In my opinion, the terminology of Sapper is more appropriate for this belt on the Southeastern Highlands. Between roughly the 1000 m. and possibly the 2000 m. to 2200 m. contours lies the oak-pine belt ("coniferous forest" of Standley and Steyermark and Steyermark and "dry oak and pine forest" of Sapper). Again the Sapper terminology seems more appropriate. Not recognized by Sapper as occurring on the Southeastern Highlands, but plotted by both Standley and Steyermark and by Steyermark is a third belt, the "temperate-cold upland forest" of elevations above the 2000-2200 m. contour.

Of these three belts the lowermost offers the greatest diversity in cover. Within this belt may be found tall-grass, prairie-like plains (Pl. II, Fig.1), short-grass plains (Pl. I, Fig. 1) , dense thickets of chaparral-like shrubs (Pl. II, Fig. 2), mixed shrub and grassland cover (Pl. I, Fig. 2), occasional stands of scrubby forest in which the *jicaro* (gourd) tree is the main element, and, near its upper limits, oak groves and a few open, pine parklands. Along the larger water courses a riparian forest (Pl. III, Fig.1) is not infrequent.

Even for a plant ecologist it would be no mean undertaking to present a clear picture of the patchwork cover-pattern of the Southeastern Highlands and especially of that of the lowermost belt. Numerous archeological sites within the region indicate that it has been occupied over a considerable extent of time, and the modification in the cover-pattern wrought by pre- and post-Columbian cultures is difficult to estimate. Where I have visited these uplands at lower elevations within the basin of Lago de Güija between 500-600 m. (Mongoy, Santa Catarina, and Anguiatú) it would seem that tall grasses predominate with larger cover consisting for the most part of chaparral-like shrubs, as at Anguiatú. In the Mongoy region, however, there remain remnants of a dry forest of considerable size. Along the larger streams a very narrow belt of riparian forest is generally present.

At elevations between 800-1000 m. short grasses seem to prevail. In alluvial basins such as that of Esquipulas these short grass plains are devoid of larger growth-forms, though on knolls above the general basin levels oak groves (these merely fringe the upper boundary of this lower belt) and open pine forests may occur. Aside from these alluvial basins most of the higher levels of the lowermost vegetational belt appear to support short grasses with chaparral, either scattered or in dense thickets, and cacti, especially of the prickly-pear type, as the dominant cover. Along the larger permanent streams a riparian forest may be present, but this forest is always considerably scrubbier than those of lower elevations.

Throughout this grass and shrub steppe and chaparral belt the seasonal aspects of the vegetation are varied indeed. During the dry season, from January into May, the vegetation becomes increasingly drier and by the end of that season the countryside is a monotonous brown and yellow. Inasmuch as the land is largely given over to grazing, the burning of pasture lands is frequent, but to one acquainted with other cattle lands in Guatemala burning is not so extensive as one might expect. Following the first rains in May, the fresh grass and leaves on the stunted trees and shrubs give the landscape a greenness that suggests far more mesic conditions than actually prevail. Only along the larger streams where such crops as corn, sugar-cane, rice, beans, a little coffee, and plantain are grown and the gallery-like forest prevails does the seasonal aspect of the landscape remain relatively unchanged.

The cover of the dry oak and pine belt is considerably more uniform than that of the lower belt. In general, this belt supports three major types of cover. Occurring most abundantly are the virgin-like forests of oak and pine. The distribution of these two within the forests is extremely uneven and apparently unpredictable. In places one encounters forests of almost pure oak which are, for the most part, rather scrubby in appearance, hung with quantities of Spanish moss (Pl. III, Fig. 2), and with a deep mantle of dried leaves on the forest floor. Again, and generally at higher elevations, the forests may be almost pure stands of pine (Pl. IV, Fig.1) which, not infrequently, are open and parklike. But most commonly the wooded areas of this belt support a mixed forest type. A second cover type in this belt consists of the open steppe lands of short grasses which may or may not be the result of clearing off the forest. On such grasslands, most frequently encountered in alluvial basins, scattered groves of oak are apt to occur (Pl. III, Fig.2). Finally, on land that is recovering from more recent clearings, a dense *monte* of scrubby oak, low shrubs, blackberry, and the like is present.

This belt is used primarily for pasture. Owing to the fact that the relief is considerably higher than at lower elevations, the hillsides are for the most part given over to pasturelands and forest growth. Agriculture is restricted to the level basin floors, especially along the stream courses, where beans and corn occupy most of the cleared land.

At levels above about 2000 m. the "temperate-cold upland forests" of Steyermark prevail. This forest, limited in extent and occurring only on the crests of some of the higher volcanoes and on the high block between Guatemala City and Jalapa, is a mixed type in which pine and oak are conspicuous features. This forest has recently received the attention of Steyermark (1950). In general, it is a wet forest in which bromeliads and other parasites are conspicuous elements and which, with the deep layer of wet leaf mold, supplies the herpetofauna with a cloud-forest-like environment.

Much of this forest has been cut, and indeed cutting continues at the present time (Pl. IV, Fig. 2). In clearings corn is planted and cattle are pastured on the short grasses and small herbs that reclaim abandoned cultivated plots. As noted previously, so humid is this zone that corn is normally planted in the middle of the dry season, and its early growth is dependent entirely upon moisture received in the form of heavy night dews.

Viewed as a whole, the cover of the Southeastern Highlands is, with the exception of the localized temperate forest, distinctly of the subhumid type. It presents an extremely patchwork pattern that has most probably resulted from the agricultural activities of pre-Columbian man and the grazing and lumbering, and to lesser extent agricultural, industries of Europeans.

THE HERPETOFAUNA OF THE SOUTHEASTERN HIGHLANDS

Any zoogeographic analysis, either of a systematic group or of a fauna of a region, must consider two major items, (1) the nature of the group or the fauna and its affinities, and (2) its local distribution. Only when such basic data are at hand, is it possible to treat problems of origin, distribution through space and time, and, in the case of regional analyses, the zoogeographic role of the area under consideration. The herpetofauna of the Southeastern Highlands is an agglomeration of amphibians and reptiles that is so small, so simply distributed, and so relatively well-known in its individual affinities that the treatment of these basic data is relatively easy and in only a few instances is analysis difficult. Of especial significance, however, is the depauperate nature of the herpetofauna. In standing out as an exceptional region with reference to this feature a number of problems are posed. Why, though annectant to the Pacific and Caribbean versants and the Southwestern Highlands of Guatemala, each of which possesses its own individual herpetofauna, have so few species of reptiles and amphibians invaded the Southeastern Highlands? What is there about the southeast that makes it so unfavorable to these groups? What sorts of species do occur there and from what sources have they been derived? In order to explain these and other questions it is necessary to examine the distribution of amphibians and reptiles in the southeast and to explain their extralimital associations, if any. I shall proceed with a few general statements concerning the nature of the herpetofaunal assemblage in the southeast and its relation to adjacent faunal units.

Nature and Affinities of the Herpetofauna

As has been noted but 59 forms have been taken within the limits of the Southeastern Highlands. To find an area within the American tropics of size and with vertical limits comparable to those of the Southeastern

TABLE I

The actual and relative (Amphibia = 1.0) number of forms of Amphibia, Sauria, and Serpentes known from different areas in northern Central America

Region	Groups	Actual Number	Relative Number
Alta Verapaz	Amphibia	34	1.0
	Sauria	38	1.1
	Serpentes	56	1.6
El Salvador	Amphibia	23	1.0
	Sauria	25	1.1
	Serpentes	42	1.8
Southeastern Guatemala	Amphibia	26	1.0
	Sauria	21	0.8
	Serpentes	12	0.5

Highlands yet supporting so small a herpetofauna as does this region would undoubtedly prove difficult. Alta Verapaz to the north, for instance, is only about half as large, if elevations comparable to those occurring in the southeast alone are considered, yet between elevations of 500 and 2500 m. the Alta Verapaz herpetofauna is over 50 per cent larger than that of the Southeastern Highlands (data from Stuart, 1950: Table I). Similarly, the Pacific versant of Guatemala between 500 and 2000 m. is only half as large as the region under discussion, and its fauna is likewise 50 per cent larger (unpublished data). Adjacent El Salvador, which within the elevation encountered in the southeast is probably of about equal size, supports a fauna of about 65 forms (data from Mertens, 1952), and thus, the size of its fauna is closer to that of the Southeastern Highlands than to that of the other two regions.

It is doubtful that this impoverishment of the southeastern herpetofauna is entirely real. It should be emphasized that no fewer than 26 species of amphibians occur within the region while the lizards number only 20. The great discrepancy lies in the snakes, of which but 12 species are known. So obvious is the absence from my collections of such highly tolerant and wide-ranging genera as *Masticophis*, *Spilotes*, *Drymarchon*, *Lampropeltis*, *Rhadinaea*, and *Crotalus*, in addition to the general scarcity of what few forms were secured, that one is led to suspect that factors other than the natural environment have brought about the impoverished condition of the snake fauna. Indeed, such forms as *Masticophis m. mentovarius*, *Bothrops a. asper* and *Crotalus d. durissus* are well known to the inhabitants of the region. Table I indicates the divergence in the composition of the known herpetofauna of the southeast from that of nearby areas.

It is true that many forms that are widespread throughout the lowlands of most of Central America do not encounter elevations within the limits of their tolerances in the southeast. Many species not present in the southeast, however, elsewhere ascend to elevations well within the limits found at lower levels in the southeast; these are characteristically grasslands or open forest types on both the

Caribbean and Pacific versants. The genus *Bolitoglossa*, *Eleutherodactylus rugulosus (s. l.)*, *Anolis lemurinus* subsp., *Corythophanes*, *Leptophis*, and *Tropidodipsas* are all conspicuous absentees at lower elevations. Similarly, at higher elevations some relative of *Magnadigita morio*, *Bufo bocourti*, and the genus *Rhadinaea* should, it would seem, find suitable habitats. A good share of the apparent impoverishment of the snake fauna, especially, may be owing to cultural factors which will be discussed later. I venture to predict, therefore, that with further study, the herpetofauna of the Southeastern Highlands will prove to be somewhat larger than it is now known to be. Nevertheless, the very nature of the species that comprise that fauna suggests that in comparison with adjacent regions it is at best depauperate.

In a previous paper I have noted that three distinct herpetofaunal assemblages may be recognized in northern Central America in general and in Guatemala in particular (Stuart, 1950: 69-79). In outline form these assemblages may be arranged as follows:

- Lowland assemblage
  - Pacific assemblage
  - Caribbean assemblage
- Plateau assemblage

About 50 per cent of the lowland assemblage of the Southeastern Highlands is composed of forms common to both the Pacific and Caribbean assemblages and widely distributed throughout the lowlands of not only all or much of Middle America but in some instances parts of South America as well. Typical examples of such forms are:

Bufo marinus
Bufo valliceps
Engystomops pustulosus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Anolis sericeus
Basiliscus vittatus
Ctenosaura similis
Cnemidophorus d. deppi
Mabuya m. alliacea
Kinosternon cruentatum

The above group seems to be well distributed over the southeast to elevations of about 1000 m., though some species ascend above that level.

A second group of lowlanders, comprising over 30 per cent of the lowland assemblage, includes forms which are (1) representatives of genera or species groups that are essentially members of either the Caribbean or Pacific assemblages or (2) are vicarious representatives on either versant of widespread species groups. Caribbean forms include:

Hyla staufferi
Hyla m. martini
Anolis tropidonotus
Ameiva u. hartwegi
Sciencella c. cherriei
Sphaerodactylus g. glaucus
Storeria d. tropica

Among the Pacific representatives may be mentioned:

Oedipina taylori
Bufo luetkeni
Hyla robertmertensi
Ameiva u. parva
Phyllodactylus eduardofischeri
Drymobius m. occidentalis

For the most part these groups of lowlanders are restricted to the fringes of the Southeastern Highlands on their respective sides. Exceptions to this generalization will be discussed later in this paper.

The Plateau assemblage is represented in the southeast by a group of forms that are either the same or close relatives of species that are members of the herpetofauna of the Southwestern Highlands and higher elevations of the Pacific versant and which spill onto the Las Nubes and Soledad Grande blocks in the northwestern part of the southeast. All are confined to elevations generally above 1700 m. This group includes:

Pseudoeurycea exspectata
Plectrohyla cotzicensis
Plectrohyla guatemalensis
Hypopachus barberi
Anolis c. crassulus
Sceloporus m. smaragdinus
Barisia m. fulva
Thamnophis c. fulvus
Geophis rhodogaster
Bothrops godmani

It will be noted that most of the above are present not only in the southwest and southeast, but are generally distributed over the highlands of northern Central America and Chiapas, and in the case of *Bothrops godmani* as far south as Panama. It would not be surprising should future more intensive collecting on the Las Nubes and Soledad Grande blocks reveal the presence of other common Southwestern Highland items, such as *Bufo bocourti, Rhadinaea godmani,* or *Tropidodipsas fischeri.*

It is to be noted that, with the exception of *Pseudoeurycea exspectata,* known only from its type locality, no species included in the assemblages listed above is endemic to the Southeastern Highlands. If endemism is to be encountered in the southeast it must be sought in a group of forms which, on the basis of present knowledge, cannot be allocated to any one of the previously mentioned assemblages. This group is difficult to analyze inasmuch as there is little uniformity in either the genetic affinities or geographic patterns of the forms of which it is composed. The assemblage is made up of:

Bufo coccifer
Bufo ibarrai
Hyla walkeri
Ptychohyla spinipollex
Hypopachus championi
Sceloporus lunaei
Sceloporus squamosus
Sceloporus v. olloporus
Cnemidophorus s. motaguae
Gymnophthalmus s. birdi
Scincella incerta
Leptodeira rhombifera

Such forms as *Sceloporus squamosus, Sceloporus v. olloporus,* or

Cnemidophorus s. motaguae occur at elevations ranging roughly from sea level to about 1500 m. as a maximum, whereas others, including the bufos, *Hypopachus championi,* and *Sceloporus lunaei* are somewhat more upland in their distributions, ranging from 1000 m. to possibly 2000 m.

Horizontally, the geographic limits of the group are extremely diverse. *Scincella incerta,* for example, occurs in most of northern Guatemala, both on the Pacific and Caribbean versants, at intermediate elevations. *Bufo ibarrai* is known only from the oak-pine zone above 1500 m. in central Guatemala. Its closest relative, *Bufo coccifer,* occurs from the southeast southward to Costa Rica. *Hypopachus championi* and *Sceloporus lunaei* have coincidental ranges from central Guatemala southward to El Salvador and Honduras. *Sceloporus squamosus* has much the same range except that it descends onto the Pacific coastal plain from eastern Chiapas to Nicaragua. *Sceloporus v. olloporus* and *Leptodeira rhombifera* are also almost coincidental geographically, ranging from central Guatemala southward to Costa Rica and El Salvador, respectively, and are entirely Pacific except in the northern part of their range, where they occupy dry valleys on the Caribbean versant. *Cnemidophorus s. motaguae* extends from the Grijalva Valley of Chiapas southward through the dry environments of central Guatemala to El Salvador. In fact, insofar as we understand these species, about the only geographic feature that they have in common is their occurrence at intermediate elevations on the Southeastern Highlands.

In their genetic affinities the members of this group are less diversified. In a recent paper (Stuart, 1953) I have shown that the following find their closest relatives in southern Mexico:

Bufo coccifer
Bufo ibarrai
Hypopachus championi
Sceloporus squamosus
Sceloporus v. olloporus
Cnemidophorus s. motaguae
Leptodeira rhombifera

It is not clear in all cases in which direction evolution and dispersal have proceeded. In the case of *Sceloporus squamosus, Sceloporus v. olloporus,* and *Cnemidophorus s. motaguae* it is fairly evident that dispersal and evolution have proceeded from north to south, whereas in the case of the bufos, *Hypopachus championi,* and *Leptodeira rhombifera,* though the same may be true, it is far less certain. All of this group have apparently utilized the Grijalva-Negro-Motagua dryland corridor (Stuart, 1953) in moving either to the north or to the south.

Ptychohyla spinipollex and *Gymnophthalmus s. birdi* and possibly *Sceloporus lunaei* appear to have been derived from forms or groups that are confined essentially to the Pacific versant of Central America. *Ptychohyla spinipollex* is the sole Caribbean representative of a hylid group which I suspect is fairly uniformly distributed along the Pacific slopes from Guerrero southward at least to El Salvador. *Gymnophthalmus s. birdi* is the only Caribbean representative of the genus north of Panama. *Sceloporus lunaei* is apparently most closely related to the Pacific coastal form *Sceloporus acanthinus*. *Hyla walkeri* and *Scincella incerta* are still too poorly known to be allocated definitely, but it may be noted that the former is, with *Hyla bocourti* of Alta Verapaz, most closely related to the *Hyla eximia* group of the Mexican plateau.

It has been indicated that if endemism occurs in the southeast, it is to be sought in this group of forms. A consideration of these shows very definitely that none is restricted to the Southeastern Highlands as herein defined. In discussing the morphology of the region, however, it was noted that the Southeastern Highlands of Guatemala are probably, in a large measure, merely a portion of a more extensive upland region that may extend at least to the Honduran Depression. In fact I should not be surprised if future investigation extended it to southern Nicaragua.

On the basis of what is known of the herpetofauna of intermediate elevations of Honduras and of better-known El Salvador (Dunn and Emlen, 1932; Schmidt, 1933 and 1936; Mertens, 1952) there is considerable coincidence with the fauna of southeastern Guatemala. It is indicated, therefore, that faunally as well as physically the uplands of western and northern Honduras and El Salvador represent a southern continuation of the Southeastern Highlands of Guatemala. Viewed in this light a number of the species previously discussed may prove to be endemic or near-endemic to this larger region. Even in those instances in which forms such as *Hypopachus championi*, *Sceloporus v. olloporus*, or *Leptodeira rhombifera* extend well beyond the limits of this larger region, it does not seem improbable that the plateau lands of middle Central America may have served as their center of origin. Certainly, it does not seem illogical to suggest that autochthony is to be sought in this larger and more stable upland region rather than in narrow valleys (e.g., the Negro or Motagua to the north) or on much less stable coastal plains (i.e., Caribbean and Pacific).

From the foregoing it might appear that the fauna of the southeast and/or its southern extralimital extension cannot be sustained as a distinct faunal unit. It appears, rather, to be a depauperate and miscellaneous assortment of some of the more tolerant forms more typical of adjacent assemblages together with a number of very wide-ranging species and a very few endemics or at least possibly autochthonous forms. It is my opinion, however, that these very features give character to the agglomeration and sustain its individuality.

Much has been written concerning the principles on which zoological regions or faunas should be defined. Wallace (1876: I, 54) laid down the basic principles for zooregionality, endemism, and absence from a suitable region without the presence of physical barriers. To these I should certainly add such features as relative abundance of individuals and the nature of the faunal assortment. These principles apply to both region and fauna. The nature of faunas mirrors differences in environmental conditions from place to place, and it is these differences that have led to regional classifications, be they zoogeographic regions, biotic provinces, life zones, or biomes. I believe, therefore, that the herpetofauna of southeastern Guatemala and its annectant regions to the south possesses unity and distinctness and is worthy of recognition as a faunal entity.

Some years ago I essayed an analysis of the biotic areas of Guatemala (Stuart, 1943), but made no effort to allocate these uplands of the southeast. I believe now that they constitute at least a part of a distinct biotic region for which, for the benefit of those who believe in the usefulness of such units and who care to refer to them by name, I suggest the term Esquipulan Biotic Area.

Local Distribution of the Herpetofauna

It has been indicated that three major vegetation belts occur in the southeast, that is, the shrub steppe and chaparral, the oak-pine forest, and the temperate upland forest. Inasmuch as the vegetation might be expected to present the most readily recognizable manifestation of a number of environmental features, some correlation between it and herpetofaunal assemblages should be apparent. In only a very general way, however, is there coincidence between the two. In fact I have previously pointed out that there is little reason to expect coincidence in the geographic patterns of vegetation and reptiles and amphibians, or, indeed, in the patterns of amphibians and reptiles alone (Stuart, 1950: 19-21). As a generalization, the lowest and highest zones support fairly distinct agglomerations, but the oak-pine belt, in addition to a few forms that appear to be restricted to it, represents a region of some overlap between the more tolerant forms of the lowest and highest zones.

The most distinct herpetofaunal break on the Southeastern Highlands falls along roughly the 1000 m. contour, which is the generalized lower limit of the oak-pine belt. Here no fewer than 24 of the 37 species that might be classed as lowlanders drop out. These 24 forms include not only Caribbean and Pacific elements restricted to their respective fringes of the uplands but a number of species that are generally distributed over the southeast below this level. Some of the more conspicuous of the forms reaching their upper limits at this contour are:

Bufo valliceps
Bufo luetkeni
Hyla robertmertensi
Hyla m. martini
Anolis sericeus
Ameiva undulata subsp.
Cnemidophorus s. motaguae
Mabuya m. alliacea
Kinosternon cruentatum
Leptodeira rhombifera

Below the 1000 m. contour there appears to be a minor break, probably in the neighborhood of the 800 m. level. The lower elevations are encountered only on the fringes of the uplands, and though I could not determine with certainty the exact upper limits on several species, I know that they are between 750 m. and 1000 m. Here I should include:

Ctenosaura similis
Cnemidophorus d. deppei
Boa c. imperator
Conophis p. pulcher

Similarly, above 1000 m. there is a minor break at about 1400-1500 m. or slightly higher which delimits most of the remainder (13) of the lowlanders. Among these may be mentioned:

Bufo marinus
Engystomops pustulosus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Phyllodactylus eduardofischeri
Basiliscus vittatus
Sceloporus squamosus
Stenorrhina freminvilli

Because I was unable to make very complete studies on the limits of species occurring above 1500 m. the exact vertical distributions of the uplanders cannot be given with any exactitude. Nevertheless, from what data are at hand it appears that the major faunal break for the true highlanders probably occurs in the neighborhood of the 2000 m. contour, and these are thus confined to the temperate forest belt. Species known only from above that level in the southeast include:

Pseudoeurycea exspectata
Plectrohyla cotzicensis
Plectrohyla matudai
Sceloporus m. smaragdinus
Barisia m. fulva
Thamnophis c. fulvus
Geophis rhodogaster
Bothrops godmani

Conversely, there is another group of species at moderate and intermediate elevations in the southeast and to which reference has already been made. Though their exact upper limits are not known, they do not range above the 2000 m. level. Here might be mentioned:

Bufo ibarrai
Ptychohyla spinipollex
Plectrohyla guatemalensis
Rana macroglossa
Hypopachus barberi
Sceloporus lunaei
Scincella incerta

Several other species, *Bufo coccifer* and *Hypopachus championi*, though definitely uplanders, reach their upper limits considerably lower, neither being known from elevations above 1500 m. The lower limits of the group confined to moderate and intermediate elevations in the southeast are extremely variable. The great majority, e.g., *Plectrohyla guatemalensis* and *Hypopachus barberi*, do not appear to descend below about 1500 m., if indeed they go that low. In contrast *Bufo coccifer*, *Hypopachus championi*, and *Sceloporus lunaei* descend to 950 m. It is apparent, therefore, that this very unevenly distributed group of species is to be considered inhabiting the oak-pine zone, even though there is not complete coincidence between the boundaries of that vegetation belt and those of the several species assigned to this group.

The local distribution of species within each of the three vegetation belts is not particularly complex. True, the agricultural, grazing, and, to a lesser extent, lumbering industries in the region have combined to produce a complex environmental mosaic, especially insofar as minor habitat-types are concerned. As I have noted in an earlier paper (Stuart, 1950: 38-42), however, reptiles and amphibians in most instances are not very specific in their selection of these minor habitats.

At lower elevations, that is, within the levels occupied by the lowland assemblage, two basic terrestrial habitat-types may be recognized: the open grasslands, with or without scattered low trees and shrubs, and the forest. The grasslands vary from clean steppe and savanna cover, through steppe and savannas with scattered desert shrubs or *jicaro* or acacia groves, to the densely tangled *monte* of low shrubs, saplings, and vines that is so conspicuous a feature of abandoned clearings. The forest habitat-type includes the few oak groves that occasionally occur here, pine forests, mixed oak and pine, and the broadleaf riparian forests.

On the grasslands proper few species of reptiles are encountered, and these occur in very small numbers. *Cnemidophorus d. deppei* and *Cnemidophorus motaguae* are the only strictly ground forms found in such areas. Where rock walls, a conspicuous cultural feature throughout the southeast, run across the grasslands, on the other hand, *Sceloporus v. olloporus*, *Sceloporus squamosus*, *Sceloporus lunaei* (above 950 m.), *Anolis sericeus*, and *Mabuya m. alliacea* appear. In this case it is obviously some environmental ingredient offered by the walls that enables these species to inhabit the otherwise coverless grassy plains. The same condition obtains where desert shrubs and low trees are present on grasslands. The cnemidophori are here far more abundant, but they remain the only strictly ground forms. Similarly, in rock walls or on *pedregal* such as was encountered on the slopes of Volcán Suchitán in the vicinity of Santa Catarina Mita the saxicolous forms noted above occur in considerable numbers. Insofar as actual numbers of individuals are concerned the *monte* supports one of the largest saurian populations in the southeast, though this is restricted to the cnemidophori and *Anolis sericeus*. Forest margin areas, which present about the same environmental conditions as the *monte*, seem to be the most favorable of the more open habitat-types insofar as reptiles are concerned. Here, especially where the margins of scattered oak groves are concerned, the saurian population is as high as is encountered anywhere at lower levels. The species are the same as those mentioned as occurring in rock walls on open grasslands together with the cnemidophori, and in addition to these the presence of shed snake skins suggests that the ophidian population is about as high as anywhere in the lower vegetational zone. It is entirely possible that the rock walls invariably found in such locales play an important role in offering cover for snakes and lizards alike.

The scattered oak groves just below the 1000 m. level support a reptilian fauna not very different from that of the forest margin, but the total population is very much smaller. The forest floor with its thick mantle of leaves offers conditions favorable to *Mabuya m. alliacea, Scincella c. cherriei,* and *Gymnophthalmus s. birdi.* Pine forests are about as sterile as are the open grasslands. In one pine grove near Esquipulas to which I devoted the greater part of one morning's collecting I encountered only three specimens of *Sceloporus v. olloporus,* and I had little better success in the occasional oak-pine groves at these lower elevations. Riparian forests in this lower belt, on the other hand, seem to present an especially favorable environment for reptiles. In such locales one encounters *Basiliscus vittatus,* always an aquatic margin type, all three species of *Sceloporus, Mabuya m. alliacea, Anolis sericeus,* and *A. tropidonotus. Ameiva undulata* subsp. is restricted to this environment, together with stream amphibians to be noted later. Along the edges of such forests cnemidophori are particularly abundant. In this connection the local distribution of *Ameiva undulata* in Guatemala presents an interesting pattern. Wherever the species occurs with *Ameiva festiva* it is a grassland form, while *A. festiva* is restricted to the forest. But wherever *A. festiva* is lacking, *A. undulata* never invades the grasslands, but is confined to the forest environment.

Of the aquatics (aquatic breeding), pond types are by far the most common amphibians in the belt of grass and shrub steppe. Permanent ponds and lakes are scarce in the southeast, but in such as do occur *Rana pipiens* and *Bufo marinus* are present throughout the year. With the onset of the wet season, when rain ponds develop in depressions on the grasslands, the seasonal breeders make their appearance. Among the commonest of these in the southeast are *Bufo coccifer, Leptodactylus labialis, Engystomops pustulosus, Hyla baudini, Hyla staufferi,* and *Hypopachus championi.* At Esquipulas I was fortunate enough to hear fine choruses of all these species. In lesser numbers in such environments one finds *Bufo valliceps, Hyla m. martini, Hyla robertmertensi,* and *Leptodactylus melanonotus.* Lotic species are few at lower elevations with only *Rana palmipes, Rana macroglossa,* and *Leptodactylus melanonotus* being more representative of running than of standing water. Of aquatic margin snakes *Leptodeira a. polysticta, L. rhombifera,* and *Drymobius margaritiferus* subsp. may be mentioned. The former two are not uncommon around frog breeding ponds at night.

The oak-pine belt, with its mixture of highlanders, lowlanders, and restricted forms, supports a fauna not very much smaller than that of the lower belt. Yet aside from breeding amphibians, populations of the individual species are the smallest encountered in the southeast. In its lower section, that is below 1500 m., the lowlanders are distributed ecologically in the same fashion as in the grass steppe and chaparral belt. Such open grasslands as occur are devoid of reptilian life. In *monte* and forest margin habitats one encounters such species as *Sceloporus lunaei, Sceloporus squamosus,* and *Stenorrhina freminvilli.* In oak or oak-pine forests *Sceloporus lunaei* occurs in small numbers, but collecting in stands of pure pine yielded nothing.

Among the aquatics the following pond breeders again make up the bulk of the amphibians:

Bufo marinus
Bufo coccifer
Engystomops pustulosus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Hyla staufferi
Hypopachus championi

From the lotic environment in the lower part of the oak-pine belt I secured only *Rana macroglossa.*

The upper part of the oak-pine belt is largely in forest with pine predominating, though wherever lumbering has been carried on, oak and scrubby second-growth often form dense thickets. In these latter an occasional *Sceloporus lunaei* may be seen, and I also secured or recorded *Scincella incerta* and *Leptodeira a. polysticta* from the same environment.

At this level standing water is largely confined to scattered, very local depressions and occasional ponds which have been formed as clay is removed for adobe manufacture. I found *Bufo ibarrai, Hyla walkeri,* and *Hypopachus barberi* breeding in such spots. At about this level the lotic environment begins to attain its maximum development, and the specialized stream hylids make their appearances. Apparently restricted to the lotic environment between 1700 and 2000 m. are *Ptychohyla spinipollex* and *Plectrohyla guatemalensis,* both of which occur with the more tolerant *Rana macroglossa.*

The temperate forest belt above 2000 m., of course, supports the small but very distinctive highland fauna. Here mountain meadows make up the grassland habitat proper. On these grassy plains I found no species of either reptile or amphibian, and I suspect that this environment is most probably cultural rather than natural. In recent clearings and along the forest margins one encounters conditions of cover similar to the *monte* of lower elevations. Here *Sceloporus m. smaragdinus* is abundant, and *Anolis c. crassulus* and *Barisia m. fulva* were both secured, though in much smaller numbers. Among the snakes *Geophis rhodogaster* and *Bothrops godmani* appear to be confined to heavier cover.

Within the forests proper the fauna seems to be small with respect to the number of both species and individuals. In the pine or pine mixed with oak I found only *Sceloporus m. smaragdinus* and *Anolis c. crassulus.* It is not improbable that the broadleaf forest supports a somewhat larger fauna, but I was able to spend too few hours collecting in this habitat to describe it with any certainty. I feel reasonably sure that the arboreal *Abronia* occurs there, while the bromeliad forms *Magnadigita* sp. and, when not breeding, *Plectrohyla cotzicensis* and *Plectrohyla guatemalensis* have been secured there. In the rubbish of the forest floor *Pseudoeurycea exspectata* is apparently common.

Standing water at these high elevations is confined to occasional depressions around springs, and from these I have taken only *Rana* *pipiens*. The lotic forms in this zone appear to be *Plectrohyla matudai*, *Plectrohyla cotzicensis*, and *Rana macroglossa*. *Thamnophis c. fulvus* is restricted, as it is throughout the Guatemalan highlands, to the aquatic margin habitat at these higher levels.

In summarizing the local distribution of the herpetofauna on the Southeastern Highlands two features of especial significance should be noted. First, two very distinct faunal elements clearly characterize two just as distinct faunal belts, that is, the temperate forest above 2000 m. and the shrub steppe and chaparral below 1000 m., though a few of the forms of this lower zone do invade the margins of the oak-pine belt. The former group of species has been drawn largely from the highlands to the north and west, the latter from the adjacent lowlands. The vertical limits of the species inhabiting the oak-pine belt, in contrast, are extremely variable. Furthermore, the geographic and genetic affinities of this group are, for the most part, obscure and, therefore, pose problems as to the role played by the Southeastern Highlands in the origin, history, and extant distribution of the group. Second, it will be noted that within each of the three belts the strictly terrestrial herpetofauna is largely a forest or forest-margin type, while the great majority of the aquatic forms, except at high elevations where standing water is unusual, are pond inhabitants. This condition suggests that the herpetofauna has been drawn in a large measure from forested regions of low to moderate relief.

DISCUSSION AND CONCLUSIONS

In the presentation of the foregoing data various problems have either been formulated or inferred. Certainly, the nature of the southeastern herpetofauna and especially its impoverished condition requires some comment and explanation. Once the nature of the fauna is understood and its local distribution summarized, problems relating to its historical aspects, particularly its origin, may be attacked. And, finally, with these data serving as a background the zoogeographic role of the region inhabited by that fauna may be discussed. In modern zoogeography these are the ends toward which regional studies are primarily directed. As early as 1902 Ortmann criticized the older school of zoogeographers to whom static descriptions of regions and faunas constituted an end in itself. Though we know today that Ortmann's scorn of such descriptions and analyses was unwarranted, for they form the requisite data on which interpretive studies are based, he was channeling zoogeography toward a modern concept of its scope and aims when he stated (1902: 269, n. 3) that "... the *historical union* [*sic*] of past and present distribution is the purpose of zoogeographic study."

Thus, modern geographic field investigations with laboratory analyses not only warrant but demand interpretation and explanation.

Factors Influencing the Composition of the Herpetofauna

The most perplexing feature of the southeastern herpetofauna is its depauperate condition. It has been indicated that some of this may not be real, but there can be no question that, in view of the varied habitats present in the southeast, its herpetofauna is certainly much smaller than might be anticipated. Two factors have apparently been active in producing this condition, the natural features of the environment, both past and present, and the more recent cultural activities of man.

Of the natural features that appear to have been most active in molding the southeastern herpetofauna, those of the past appear to have been paramount. I have previously suggested (1950, 1951) that Pliocene uplift was responsible for differentiation into highland and lowland agglomerations of some of the amphibian and reptilian groups present at that time in northern Central America, especially through Chiapas and southwestern Guatemala. Furthermore, this same uplift and its accompanying climatic changes permitted invasion of the region by groups that had already differentiated to the north in Mexico. South of the Río Motagua uplift appears to have been less intense than to the north and west. Thus, only about 10 per cent of the terrain to the south lies above 1500 m. as compared with about 90 per cent above that elevation to the north. This might permit in the south a far greater degree of gene flow between the uplifted populations and their parent populations of lower elevations than in the north. As a result the lower uplands of the south could never have attained the stature of the higher plateaus to the north as a center of differentiation. Furthermore, the environments present at high elevations in the north which afforded habitats for northern entrants were never developed in the south. Similarly, uplift, though apparently general, was more intense in some regions than in others, with the result that high mountain ranges rimming the southeast were formed, especially to the north. These undoubtedly greatly reduced the amount of precipitation entering the region, particularly from the north and east. It is not improbable, therefore, that many groups which were essentially mesic types were unable to invade or persist in the southeast even in the absence of other physical barriers. Hence in not affording conditions suitable for any great amount of local differentiation or for invasion by or survival of diversified faunal elements, the Southeastern Highlands and their annectant regions were handicapped faunally speaking from the very beginning.

Of extant conditions that contribute to the depauperate condition of the fauna of the southeast, the absence of any extreme environmental conditions in the region appears, peculiarly enough, to be the causative agent. Though there is a diversity of habitat, the southeast is neither excessively mesic nor excessively xeric, neither is it particularly high nor very low. It has been noted that the greater part of its fauna appears to have been derived from that of mesic forested areas, but there is also a definite xeric element present. The fauna's major relationship is directed towards the lowlands, but, again, there is a small highland element. The region is such, however, that any forms that have developed any high degree of specialization to either mesic or xeric conditions or to either lowland or highland environments apparently do not find habitats within the range of their tolerances in the southeast. Thus, only the more tolerant of the highlanders or lowlanders or of mesic or xeric types appear to be able to cope with the "ecotone" environment presented by the Southeastern Highlands as a unit.

In illustration of this situation I have previously shown (Stuart, 1950: Table I) that over a third of the herpetofauna of Alta Verapaz, a fairly representative example of Caribbean versant types, does not ascend above 600 m., and such forms as do go beyond that level encounter mesic conditions. A similar proportion of the herpetofauna of the Pacific versant does not ascend above 600 m., and again such forms as do go to higher levels are inhabitants of a very humid environment. Except in fringing areas it must be remembered that the southeast is made up largely of terrain above the 600 m. level and this is, for the most part, semiarid.

Three major cultural activities in the southeast seem to be largely responsible for the dearth of reptilian and amphibian life in many areas: grazing and agriculture, which are most extensive below 1500 m., and lumbering, which is largely confined to elevations above that level. It is not so much the original clearing of the land for agriculture and grazing at lower elevations that appears to have diminished animal populations, for such activities produce conditions not very unlike those of the region's natural environment, that is, grasslands and brushlands, but rather the annual firing that accompanies these activities over the years. Furthermore, annual tilling and the constant disturbance of the land by herds of domestic animals certainly do not enhance the favorableness of such plots as reptilian habitats. At higher elevations clearing of the land, even where the lumbering industry is active, is far less intense than at lower elevations. Inasmuch as only the larger trees are utilized, the forests are thinned rather than cut in their entirety. The smaller human population of such upland regions similarly requires that less terrain be cleared for agriculture and grazing. As a result the forest fauna has suffered less in such areas than at lower elevations. Nevertheless, highland aquatic types have undoubtedly felt the impact of cultural activities in more than one way. Clearing has undoubtedly contributed to the severity of seasonal fluctuations in the streams, producing torrential conditions in the wet season and greatly reducing the dry season flow by reducing water storage in the soil. Contamination, especially oxygen depletion, through the dumping of sawdust, must render conditions for tadpoles intolerable in many streams, and the use of small headwater tributaries for lumber slides not only affects the stream bed, but also greatly modifies aquatic margin environments.

On the other hand such factors as the building of rock walls, the accumulations of slash, and the extension of forest conditions through the planting of bananas and coffee have provided some species with even more favorable habitats than occur under natural conditions. This has apparently permitted local growth of populations well beyond the limits that could be attained in unmodified terrain. A conceivable result of such a condition might be extermination of species not so benefited, through the tremendous competition produced by population pressure.

In analyzing the reasons for the depauperate nature of the fauna of the Southeastern Highlands all of these factors must be taken into consideration and must be treated as a unit rather than individually. But in addition to producing a depauperate fauna, these various factors, insofar as the human element is concerned, have often so modified population sizes that an analysis of such fauna as does exist is difficult.

As indicated, not all units of the fauna of the southeast are equally impoverished. The entire herpetofauna, to be in accord with that of adjacent regions, should number about 100 forms as compared with the 59 known from the area. The discrepancy in the number of forms is restricted largely to the reptiles. The amphibian fauna, in contrast, is surprisingly large. Insofar as natural conditions are concerned, amphibians, especially pond types, rarely are subjected to the unfavorable environmental conditions of the extended dry season. Given a few weeks of rainfall and terrain favorable to pond formation, amphibians can and do move about and reproduce before retiring for the remainder of the year. Lizards and snakes, in contrast, remain active throughout the year and are subjected to the brunt of the drought period. Thus, it is only natural that amphibians have been far more successful in invading and surviving in the southeast than have either of the other two groups. Even the cultural activities of man do not greatly affect the pond amphibians. Depressions in which ponds form are rarely cultivated, and should fire sweep through such an area during firing activities at the end of the dry season, the amphibians are safely aestivating. To a lesser extent lizards, owing to their small size, may in most instances seek refuge beneath stones and survive the rigors of drought and human agencies. Snakes, both because of their greater food requirements (excepting small secretive forms) and because of their size, do not find survival so simple a matter in many regions. Finally, man himself is a definite factor in the differential depletion of populations of various animal groups: Snakes are destroyed; lizards are generally tolerated; amphibians are ignored.

In view of these factors it appears that the answers to some of the questions posed are fairly obvious. The fauna is small in terms of species and frequently in terms of individuals simply because the environment of the region has not in the past presented conditions that would permit its invasion by a great number of amphibian and reptilian groups. Extant conditions both natural and those wrought by man are such that only highly tolerant forms can manage survival.

Of the invading species which have managed to survive the environmental conditions presented by the southeast, it has been noted that about 80 per cent are either wide ranging (and presumably highly tolerant) forms or are the commoner and generally more successful elements derived from adjacent lowland areas on either side of the uplands. It has further been shown that in the southeast the great majority of the reptiles of lower elevations are largely restricted to the more mesic environments of the region, that is, the broadleaf upland forest, where mulch accumulates, and riparian forests, while the amphibians occur in areas subjected to extensive flooding or pond formation during the wet season or in permanent streams. Highlanders that have invaded the southeast are restricted in their ranges owing to the fact that high terrain is not extensively distributed in the region. Finally, such autochthonous or near-endemic types as occur in the southeast have for the most part been derived from ancestral essentially dry-land forms which have found tolerable environments in the region. But it should be reiterated that such species form only a small fraction of the Southeastern Highlands herpetofauna.

Though the matter will be treated in greater detail later, it may be pointed out here that there is reason to suspect that during pluvial periods of the Pleistocene the fauna of the southeast may have been considerably larger than it is at present. With the onset of more xeric conditions, however, many forms may have been completely exterminated or have experienced a reduction of population to a near-extinction level. This may in part explain my failure to secure a number of forms (previously mentioned) expected in the region.

Origin and History of the Herpetofauna

In previous papers (Stuart, 1950 and 1951) I have essayed historical accounts of the herpetofauna of the Southwestern Highlands and of Alta Verapaz. The history of the fauna of the southeast and annectant uplands to the south does not differ from that of these adjacent faunas in its basic outline. Dunn (1931) has presented an analysis of the herpetofauna of the Americas which is now so well known that it need only be outlined at this time:

- Old Northern
    - Older element
    - Younger element
- South American
- Boreal

I have (Stuart, 1951) pointed out that yet another minor element, which I have named the Autochthonous Middle American element, appears to have developed in Middle America, one the history of which has been almost the same as that of the older Old Northern element, but which finds its closest relatives in South America rather than to the north. All these elements with the exception of the Boreal are represented in the Southeastern Highlands.

Similarly, the historical geology of middle and northern Central America during the Cenozoic is so well known that only a brief review is necessary.

1. Connection with both North and South America up to the mid-Eocene.
2. Separation from South America, mid-Eocene to mid-Miocene or possibly early Pliocene, and, since, continued contact with South America.
3. Probable separation from North America at the Isthmus of Tehuantepec during the late Miocene or early Pliocene.

4. Warm, moist, moderately elevated upland until Pliocene.
5. Uplift and temperature reduction beginning in Pliocene or possibly late Miocene.
6. Alternating cool and warm periods with varying degrees of humidity during the Pleistocene.

The older Old Northern and representatives of the Autochthonous Middle American elements entered Central America during the Eocene. The ancestors of the latter continued southward into South America, but left behind representatives in Middle America. The former apparently entered the region shortly thereafter. Between the time of their entrance and into the Pliocene these groups underwent differentiation, some in the north in southern Mexico and others apparently farther south. Representatives of these now present in the southeast include:

Oedipina
Magnadigita
Plectrohyla
Anolis
Basiliscus
Stenorrhina
Ninia
Geophis

With the closing of the lower Central American portal, the South American element moved northward into the region. Among these invaders might be mentioned:

Engystomops
Leptodactylus
Hyla
Sphaerodactylus
Ameiva
Mabuya

Some of this group, *Hyla* and *Cnemidophorus* for example, appear to have moved into the Mexican region, where, during the period of isolation of Central America from Mexico owing to the open Tehuantepec portal in the Pliocene, they underwent secondary differentiation. But the great majority barely entered the "Nearctic Realm."

With the temperature reductions that accompanied Pliocene uplift and that were intensified with the onset of the Pleistocene, conditions were ripe for a southward movement of northern groups. These were representatives of the younger Old Northern element together with such southern groups as may have differentiated secondarily in the north. Some of these appear to have spread southward across lowlands or through the Grijalva-Negro-Motagua desert corridor (Stuart, 1953), while others moved along highland routes. Such groups as *Ctenosaura*, *Sceloporus variabilis*, *Sceloporus squamosus*, and *Cnemidophorus* apparently followed the lowlands, while *Pseudoeurycea*, *Sceloporus smaragdinus*, *Barisia*, and *Thamnophis cyrtopsis* remained highlanders in their southward movement.

By this time all the various elements that have contributed to the herpetofauna of the Southeastern Highlands and their southern extensions were either in the region or in a position to enter the area as suitable environments were formed. As previously indicated, variations in climatic conditions through the Pleistocene seem largely responsible in determining the groups which could or could not enter the region and those which could survive once entrance had been effected. As is brought out later, certain geographic discontinuities both north and south and east and west in middle Central America indicate that the herpetofauna of the southeast has undergone, through the Pleistocene, considerable modification. During periods of extensive glaciation, when temperature belts undoubtedly descended to lower levels, certain highlanders appear to have moved southward across the region at much lower elevations than those to which they are now restricted. *Pseudoeurycea,* for example, apparently reached the mountains of northwestern Honduras while more vagile forms, such as *Sceloporus smaragdinus* and *Barisia moreleti,* moved as far south as lower Central America. Return to more moderate climatic conditions "forced" them into the higher levels to which they are now restricted and thus produced their discontinuous geographic pattern of isolated populations on mountain crests through Central America. Conversely, there appears to have been some faunal movement between the Caribbean and Pacific lowlands which probably was effected during warmer (and it is indicated much more moist than at present) interglacial periods. Certainly, the occurrence of isolated populations of such essentially Pacific versant forms as *Gymnopis m. mexicana, Enulius flavitorques,* and *Leptodrymus pulcherrimus* in northwestern Honduras, the presence of the Caribbean *Conophis pulcher* at low elevations on the Pacific, and the apparent absence of all these forms from the central part of the Southeastern Highlands suggest that they may well have occurred in the southeast in the past.

The final recession of the glaciers and the appearance of warm, dry conditions in the southeast resulted in the molding of the extant herpetofauna. Highlanders retired to the only environments available to them, those of the high blocks in the northwestern part of the region. Only the more tolerant of the lowlanders found suitable environments at lower levels. Finally, the few near-endemics or autochthonous forms seem to have developed, for the most part, from parent stocks from which they became isolated by the highlands to the north and west or with which they were but weakly connected through such tenuously suitable environments as the chain of dry valleys and basins that extends through central Guatemala.

Zoogeographic Role of the Southeastern Highlands

In consideration of its position as an upland region separating the Caribbean and Pacific coastal plains and because of its peculiar depauperate herpetofauna, it is to be suspected that the low plateau of middle Central America, of which the Southeastern Highlands represent the northern section, might have played a role of some importance in the distribution of the herpetofauna of Central America. Three features particularly seem to warrant some consideration: the uplands as a barrier to Pacific-Caribbean faunal interchanges, the role of the uplands as a pathway of north-south dispersal, and the role of the region as a center of differentiation. Unfortunately, the last must await information concerning faunas and their distributions farther south.

Reference has already been made to a Caribbean and to a Pacific lowland assemblage. Though the two are remarkably alike in their general make-up, they do display differences that render them easily separable. At the generic level, for instance, such genera as *Sphaerodactylus*, *Laemanctus*, and *Pseustes* are, in the north at least, strictly Caribbean as opposed to *Gymnophthalmus*, *Enulius*, and *Loxocemus* which are definitely Pacific. At the specific level the differences are even more pronounced, while the majority of species common to both sides are represented in either assemblage by different races. Though the nature of the fauna changes radically in southern Central America the same Caribbean-Pacific breakdown apparently obtains, at least between southern Nicaragua and eastern Panama. But unlike the north the assemblages in the south apparently cross over in eastern Panama, the Pacific element continuing into Caribbean South America and the Caribbean group crossing to Pacific Colombia.

North of eastern Panama the highland barrier breaks down in southern Nicaragua, yet, so far as may be judged from scattered collections, there appears to be little or no mixing of the two faunal assemblages in that region. It is not improbable that the mesic conditions of the Caribbean versant as opposed to xeric environment of the Pacific are instrumental in maintaining faunal differences on either side of the isthmus. Farther north in the Isthmus of Tehuantepec region the mountain barrier between the east and west sides again disappears, but climatic differences as well as a distinct faunal assemblage centered on the southern side of that narrow isthmian area seem to have prevented faunal panmixia.

As knowledge of Honduras, El Salvador, and Guatemala has increased, however, a certain amount of faunal intermixture appears locally, especially along the Pacific between western El Salvador and middle Guatemala and between the Motagua Valley of Guatemala and northwestern Honduras on the Caribbean. Though it cannot be said with certainty that some species do not occur farther south along the Caribbean, at present no data suggest that they do. In fact the ranges of several recently reviewed forms have been assumed to occur on both coasts merely on the basis of the Honduran population and widespread distribution along the Pacific to the south. Until definite Caribbean records to the south are forthcoming, the Caribbean Honduran and/or Guatemalan populations must be treated as localized Pacific elements. The following display such a pattern:

Gymnopis m. mexicana
Ptychohyla spinipollex
Phyllodactylus sp.
Coleonyx mitratus
Gymnophthalmus s. birdi
Leptodrymus pulcherrimus
Enulius flavitorques
Coniophanes piceivittus
Imantodes gemmistratus
Bothrops ophryomegas

Conversely, the following forms are entirely Caribbean except for their local occurrence along the Pacific in eastern Guatemala and El Salvador:

Hyla staufferi
Scincella c. cherriei
Dryadophis dorsalis
Elaphe triaspis subsp.
Conophis p. pulcher

It will be noted that the list of Pacific elements on the Caribbean is much larger than that of Caribbean elements on the Pacific. The reason for this is fairly obvious. Whereas xeric as well as mesic environments are available along the Caribbean in the region under discussion, the Pacific presents, except at high elevations, only drier environmental types. Thus, Pacific forms, normally subjected to the less mesic conditions of the Pacific (*Phyllodactylus, Coleonyx, Bothrops ophryomegas*), or mountain stream types (*Ptychohyla*) encounter environments within the limits of their tolerances on the Caribbean. Caribbean forms, in contrast, adapted to the more mesic conditions of the Caribbean versant, find few such environments along the Pacific slopes of eastern Guatemala and western El Salvador, and only the more tolerant species of that group have been able to survive in that region.

Only in the case of *Hyla staufferi* is it definitely known that the Pacific and Caribbean populations of these species and genera are continuous across the Southeastern Highlands of Guatemala and annectant regions to the south. Exploration of Honduras, where passes across the uplands are lower and more numerous than in southeastern Guatemala, will undoubtedly reveal other geographic continuities. On the other hand there is little reason to suspect that some forms are continuous in their distributions, especially such lowlanders as *Bothrops ophryomegas*.

It is indicated that such geographic discontinuity as may occur in these forms is of fairly recent origin. Two environmental events appear to have been responsible for such discontinuities as may eventually be proven: uplift that began in the Pliocene and is still in process, and interglacial climatic conditions of greater humidity than those of the present. The former requires no comment beyond indicating that uplift of a mere 200 m. could have produced the upland barrier that now separates the very distinct Pacific and Caribbean assemblages restricted to elevations below 600 m. in Honduras and Guatemala. If discontinuity between the Honduran and Guatemalan populations of Pacific elements and their parent populations can be established, the isolating uplift responsible for the event need not be projected into the very distant past. Similarly, if the Sangamon may be taken as a measure of climatic condition during later interglacial stages, mesic environments tolerable to Caribbean elements would have permitted a crossing to be made to the Pacific (Hibbard, 1952; van der Schalie, 1953). Thus, the Southeastern Highlands and their southern extension, while acting as a barrier separating a lowland Pacific fauna from a lowland Caribbean fauna, have been endowed, in the past, with environmental conditions that have permitted a certain degree of faunal mixture.

Just as there has been faunal movement from east to west and vice versa across these uplands, so there appears to have been a certain amount of movement from north to south. There are no data to indicate that there has been any northward movement of southern elements through the region. The southward movement of northerners or groups autochthonous to Central America, furthermore, has not been extensive, and such groups as have dispersed southward are today confined to relatively high elevations, as has been noted by Carr (1950: 579). Genera so distributed are:

Magnadigita
Pseudoeurycea
Sceloporus, formosus group
Barisia
Rhadinaea, godmani group
Bothrops, godmani group

These and other genera which may be added with future exploration do not all extend equally distant southward. *Pseudoeurycea* and *Rhadinaea* extend only into El Salvador and Honduras, *Sceloporus* and *Barisia* reach western Panama, and *Magnadigita* has invaded northern South America. The degree of their southward distribution appears to be dependent in part upon the time of entrance into Nuclear Central America and in part upon the vagility of the group. *Pseudoeurycea* is unquestionably a recent entrant from southern Mexico as opposed to *Magnadigita,* which is very probably autochthonous to Central America. *Barisia,* though also probably a recent entrant from the north, is possessed of greater vagility than *Pseudoeurycea* is.

Isolated at high elevations as these groups are, former geographic continuity must be assumed. There seems to be little question but that such continuity has existed during the several glacial stages of the Pleistocene. Though several authors suggest that the extant subtropical zone may have extended to sea level at various times during glacial advance, no such extreme climatic condition is necessary to explain the present distribution of these genera. I have noted previously that a temperature reduction of no more than about 5° would permit the majority of the highland species to move across a good part of Nuclear Central America were temperature the major factor in the distribution of these groups, as is indicated. Thus, with glacial advances and the accompanying lowering of temperature belts the northern invaders moved southward, and the final glacial retreat and elevation of the temperature belts to their present levels has resulted in the isolation of local populations on the higher peaks through middle and lower Central America.

It may be noted that representatives of these genera are not encountered on all the peaks upon which tolerable environments seem to be present. On Volcán Jalapa (Jumay), for example, no highlanders were encountered. Had Jalapa been in existence during the period of extensive Wisconsin glaciation, such forms as *Pseudoeurycea* sp. or *Sceloporus m. smaragdinus* would very probably have come in contact with it and retreated to its crest with the elevation of the "temperate zone." This suggests that Jalapa came into existence in fairly recent times or at least since the recession of the Wisconsin glaciers.

At lower elevations the Southeastern Highlands and their southern extension seem to have served in a dual capacity for herpetofaunal movements, that is, both from the Caribbean to the Pacific and southward from the Motagua Valley. I have previously indicated that some forms find their closest genetic and geographic relationships to the north in southern Mexico:

Hypopachus championi
Sceloporus squamosus
Sceloporus v. olloporus
Cnemidophorus s. motaguae
Leptodeira rhombifera

These apparently have not moved southward from the Isthmus of Tehuantepec along either the Caribbean or Pacific lowlands but, rather, through the dry-land corridor previously described (Stuart, 1953). Their opportunity to move farther southward along the drier portions of the Pacific versant was apparently afforded by the presence in southeastern Guatemala of the dry uplands which link the Motagua Valley with the Pacific.

The role of the Southeastern Highlands and their southern extension in providing a center of differentiation need not be elaborated here. The genetic and geographic affinities of the majority of the near-endemics or forms which appear to be autochthonous to the region are too poorly known to permit comment other than the rather unsatisfactory discussion that has been presented.

SUMMARY

1. The Southeastern Highlands of Guatemala are defined as an upland region between the valley of the Río Motagua and the borders of El Salvador and Honduras.
2. These highlands have an area of some 10,000 sq. km. Elevations range from 500 m. to 2600 m., with the greater part between 1000 m. and 1500 m.
3. This region has been subjected to uplift and volcanism beginning in the Pliocene, but neither process has been so intense here as in the southwest or along the Pacific versant.
4. The climate is subhumid and one of moderate temperatures except at elevations above 2000 m.
5. Three vegetation belts may be recognized in the region, a lower belt which supports short grasses, desert shrub, and chaparral, an intermediate one of oak and pine, and a high one of temperate broadleaf forest.
6. The region supports a depauperate herpetological assemblage of but 59 known forms. The snake fauna is especially impoverished.

7. The herpetofauna is distributed vertically in rough accordance with the vegetation belts; a lowland element restricted to the desert shrub and chaparral, a highland element in the temperate forest belt, and an element of obscure relationships, either near-endemic or autochthonous to the region, in the oak-pine belt.

8. The local distribution of the herpetofauna suggests that as a whole it has been derived from types characteristic of forested regions of no more than moderate relief.

9. It is concluded:

a. The lack of diversity in the herpetofauna is owing to the relatively slight amount of uplift in the region which has permitted a certain amount of gene exchange with parent populations of lower elevations, to the subhumid conditions of these uplands which present an environment intolerable to many mesophiles, and, more recently, to the cultural activities of man.

b. There is, with the exception of a poorly understood element that may prove to be autochthonous to the moderately elevated uplands of middle Central America, nothing unusual about the derivation of the herpetofauna, its history being not unlike that of assemblages previously described from Alta Verapaz and the Southwestern Highlands of Guatemala.

c. The Southeastern Highlands, now a barrier to faunal interchange between the Pacific and Caribbean lowlands, may have, in the fairly recent past, served as a bridge for faunal mixing between those two areas. The same role may have been played by the southeast in north-south faunal movements.

APPENDIX I. LIST OF COLLECTING LOCALITIES

Though my field season of 1952 was devoted primarily to a study of the Southeastern Highlands, several opportunities to examine other parts of Guatemala presented themselves. As a result, though I was in Guatemala from mid-January until mid-August, less than half my time was spent on the Southeastern Highlands. I was, however, able to visit each of my three major bases, Esquipulas, Jalapa, and Jutiapa, during both the wet and dry seasons.

Needless to say, the locality data presented in the Annotated List of Species (Appendix II) are exact only insofar as they record the centers from which I worked, and these were often as much as 30 km. from the actual sites of some of my collections. More exact data are to be found in my field notes and in the master catalogues in the Division of Reptiles and Amphibians, Museum of Zoology. In consideration of this I present a list of the localities from which data have been forthcoming from the southeast and give brief accounts of them.

Elevations of the following localities are those of the plaza in the case of villages and those of the *casa grande* in the case of fincas. All distances are air-line measurements taken from the Millionth Map of the American Geographical Society. In describing the location of smaller villages and fincas I have utilized as a point of orientation the closest large city, all such cities being on the map indicated above. My Maps 1 and 2 are also based on it, but present only those natural and cultural features pertinent to this paper. Unless otherwise indicated I visited all localities in 1952.

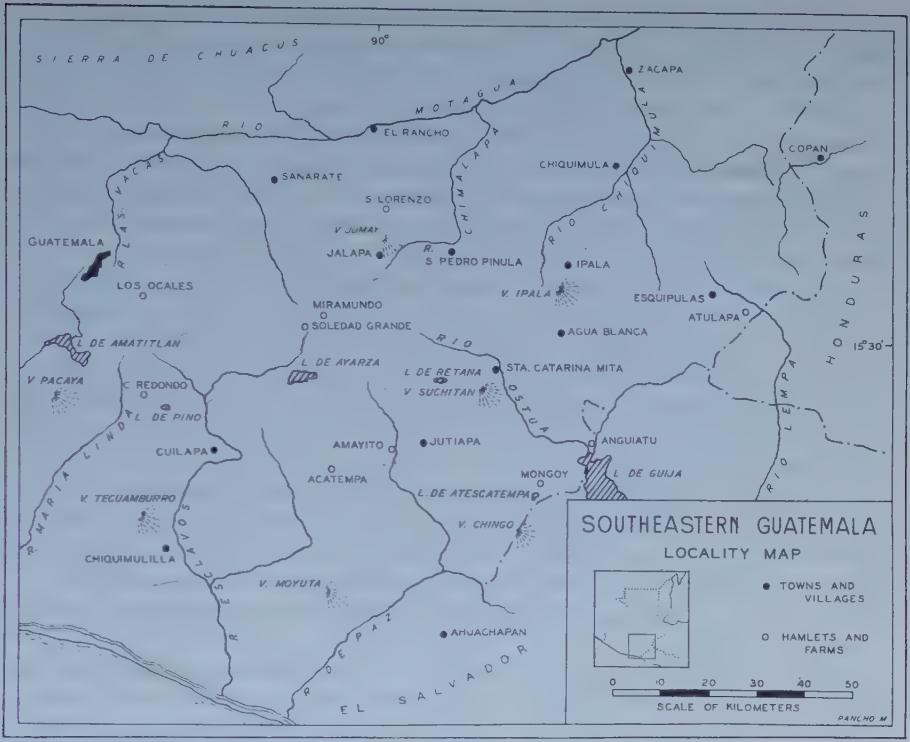
Acatempa. — A small hamlet 25 km. west of Jutiapa *(q.v.)*. Elevation, 1350 m.

Amayito. — A settlement of a half-dozen houses 8 km. west of Jutiapa *(q.v.)*. Elevation, 950 m.

Asunción Mita. — A commercial town 20 km. east and slightly north of Jutiapa. The Río Ostúa was studied at this point by members of the American Fish and Wildlife Survey. The terrain and cover are similar to those of Mongoy. A Miller locality. Elevation, 600 m. Not on Map 2.

Atulapa. — A hamlet 5 km. east of Esquipulas *(q.v.)*. Elevation, 880 m.

Cerro Redondo. — As used herein the name refers to a general region of the great government finca of the same name. In the immediate vicinity are El Rosario and Las Viñas. Most of the original vegetation has been cleared, and the land is now largely in coffee groves, pastures, cornfields, and brushy second growth. The region is rather well watered by surface streams and is the most humid part of the Southeastern Highlands. Collections were made in the region by Tashian and De la Torre, who collected at elevations of about 1100 m. I have passed through the region many times, but have never made collections in this part of the southeast.



MAP 2

El Carnero. — A small finca 7 km. west of Jutiapa in terrain similar to that of Amayito. A De la Torre locality. Elevation, 1000 m. Not on Map 2.

El Progreso. — A finca 15 km. southwest of Cuilapa near the slopes of Volcán Tecuamburro. Pacific slope forest is characteristic of the region. A De la Torre locality. Elevation, 1350 m. Not on Map 2.

El Rosario. — A finca in the Cerro Redondo district *(q.v.)*, 27 km. south and slightly east of Guatemala on the road to Cuilapa. Terrain rolling, cover largely brushland. A De la Torre locality. Elevation, 1200 m. Not on Map 2.

Esquipulas. — A village in the department of Chiquimula about 45 km. south and slightly east of Zacapa. The site of the shrine of the Black Christ, it is the religious center of most of Central America. The hamlet lies in a basin, oriented north-south that I judge to measure about 8 km. by 10 km. The basin floor is level to gently rolling, and terrain of any relief whatsoever is encountered only at the base of the surrounding mountains, which rise to a maximum of about 600 m. above the basin floor. A single stream of some size drains most of the center of the basin, and it is formed by small permanent and intermittent creeks that, though deeply entrenched, meander sluggishly through the basin. Many local rain ponds form on the basin floor during the wet season. Along the base of the mountains, especially in the south where Esquipulas is located, a number of small freshets occur. All join to form the upper course of the Río Lempa. In the vicinity of Esquipulas there are fine groves of stunted oak and open parklands of pine. The basin proper, however, supports a cover of short grass and is almost treeless. Along the larger streams a riparian forest forms a narrow band. On the mountain slopes a dense tangle of scrubby vegetation, primarily oak, obtains. Much of the basin is utilized for pasture, but along the larger streams coffee, sugar cane, and bananas are planted. Most of my collection stemmed from the immediate vicinity of the village, though some time was spent along the Río Atulapa near the settlement of the same name some 5 km. to the east. Here riparian forest conditions were encountered. My collections were made at elevations between 860 m. and 960 m. Elevation, 910 m.; March 1-15 and May 16-28.

Guatemala [City]. — The capital of Guatemala is situated at lat. 14° 38′ N. long. 90° 31′ W. For further description see Stuart (1951: 44). I collected a few amphibians on the south edge of the city on the evening of May 13, and R. R. Miller secured amphibians from many of the streams in the vicinity, these mostly tributaries of the Río Las Vacas. Elevation, 1485 m.

Jalapa. — This village, the capital of the department of the same name, lies about 60 km. due east of Guatemala. Dominated by the high Soledad Grande block to the east and Volcán Jumay to the north, the village is situated on a rolling upland that may represent a part of an ancient peneplain. The area is fairly well watered by headwater streams, all deeply entrenched, of the Río Chimalapa. A small lake to the north of the town was the site from which the major portion of my amphibian collection from the region was obtained. Most of the terrain supports a short grass cover with oak constituting the main forest type. I did little collecting in the immediate vicinity of the village, except for amphibians. Such reptiles as were secured in the region stemmed for the most part from the vicinity of San Pedro Pinula, some 15 km. to the east. Here were encountered short-grass plains with scattered desert shrub. Along the Río Chimalapa were some stretches of riparian forest. Elevation, 1380 m.; September 12-16, 1944, March 17-18 and June 7-15, 1952.

Jutiapa. — A town, the capital of the department of Jutiapa, about 75 km. east-southeast of Guatemala. It is the most important commercial town between the capital and the Salvadoran border. Most of the terrain in this vicinity is rolling and broken by a number of low volcanic cones. The region is poorly watered by sluggish streams that are little more than a series of pools in the dry season. The soils of this area are shallow and rock outcroppings are frequent. Inasmuch as agriculture and grazing are the main industries of the region, little virgin forest is to be found. Tall savanna grasses, groves of *jicaro*, and scattered dry-land shrubs constitute the main cover types. Most of my collecting in the region was done to the northwest of the village, and some time was spent along the Río Amayito some 8 km. to the west, where fine riparian forest prevails. Mr. de la Torre secured some material from El Carnero in the same general vicinity, a locality of similar environmental conditions. Farther to the west in the vicinity of Acatempa, a village noted throughout the republic for the skill of its inhabitants in pursuits of a lightfingered nature, the relief is considerably greater and oak forms the predominant cover type. From Jutiapa I collected at elevations varying 940 — 1300 m. Elevation, 950 m.; September 7-10, 1944, March 23-April 1 and July 7-11, 1952.

Laguna de Atescatempa. — A small lake 4 km. south of Mongoy *(q.v.)*. I collected here briefly, as did Miller. Elevation, 600 m.

Laguna de Ayarza. — A crater lake 48 km. southeast of Guatemala. For a full description see Holloway (in Saunders, Holloway, and Handley, 1950: 109-10). A Miller locality. Elevation, 1450 m.

Laguna del Pino. — A small lake in the Cerro Redondo region *(q.v.)*. A Miller site (Saunders, Holloway, and Handley, 1950: 111). I have passed by the lake a number of times, but have never stopped at it. Elevation, 1040 m.

Las Nubes. — A highland block just east of Guatemala. I collected here in 1949 (Stuart, 1951: 44).

Las Viñas. — A finca in the Cerro Redondo region *(q.v.)*. A Tashian locality (Tashian, 1953: 198). Elevation, 1100 m. Not on Map 2.

Los Ocales. — A small farm 12 km. southeast of Guatemala. I worked here in 1949 (Stuart, 1951: 44). Elevation, 2000 m.

Miramundo. — A hamlet on the Soledad Grande block *(q.v.)*. Elevation, about 2400 m.

Mongoy. — A sugar cane plantation 21 km. slightly south of east of Jutiapa. Most of the terrain of this section appears to be ancient lake bottom, apparently formerly connected with or actually a part of Lago de Güija. The old bottom is rimmed with uplands which, though of low elevation, are of high relief and which support a cover of desert brush. Though most of the level land in the region is under cultivation, one may encounter here patches of dry upland forest and riparian forest as well as extensive stretches of savanna grasses. While stationed here visits were made to Laguna de Atescatempa, where collections were made on the lava fields that flank the base of Volcán Chingo. For a description of the lake see Saunders, Holloway, and Handley (1950: 110). To judge by the number of uneroded cones and local lava beds much of this region appears to have been subjected to considerable volcanic activity in the fairly recent past. Elevation, 550 m.; April 15-19.

Río Atulapa. — A headwater stream of the Río Lempa that rises in the hills behind Esquipulas. Along this stream were encounterd fine stretches of riparian forest or forest-like conditions. Collections were made almost from its source to the village of Atulapa. Not on Map 2.

Río Amayito. — A medium-sized headwater stream of the Río de Paz system. It was investigated below the settlement of Amayito, where stood the finest riparian forest encountered on the Southeastern Highlands. Not on Map 2.

Río Las Vacas. — The cloaca maxima of the city of Guatemala. Many amphibians were collected here by Miller.

San Lorenzo.— A sawmill about 12 km. north of Jalapa. It is situated on the south side of an ancient mountain mass that forms the south wall of the Motagua Valley and is dominated to the south by Volcán Jumay. Most of the terrain in the immediate vicinity is of high relief, though to the south the rolling uplands of the Jalapa region begin and to the east there is a high basin. The region is well watered by streams that have carved deep gorges in the uplands. The dominant cover is oak and pine with but few pure stands. Despite lumbering activities there is some fine virgin forest in the region. Much of the land, however, has been cleared for agriculture and pasture. While here Mr. de la Torre and I climbed to the crest of Volcán Jumay (2120 m.), where recent cutting had destroyed some of the virgin forest. Most collecting in the region, however, was done between 1625 m. and 1770 m. Elevation, 1735 m.; February 9-17 and June 16-20.

San Pedro Pinula. — A small village 17 km. east of Jalapa *(q.v.)*, from which base I worked this region. Elevation, about 1100 m.

Sanarate. — An uninviting village on the rail line between Guatemala and Puerto Barrios. It lies in rugged terrain in the lower part of the oak zone and some 25 km. northwest of Jalapa. A Miller locality. Elevation, about 900 m.

Santa Catarina Mita. — A small village 25 km. northeast of Jutiapa. It is in the valley of the Río Ostúa, which is here a stream of considerable size. The hamlet is dominated by Volcán Suchitán, and the lavas from this volcano cover most of the terrain above the village. A scrubby *espinal* is the main cover of such areas. Below the village along the river there are fields of cane and coffee groves that present conditions comparable to riparian forests. Elevation, 740 m.; April 22-23.

Santa Lucía. — A farm 13 km. south and slightly east of Guatemala. It lies in the same general region as Los Ocales *(q.v.)*, and the environmental conditions of the two localities are very similar. A De la Torre station. Elevation, 1900 m.

Santa Rosa. — A small village in the upper Río Esclavos drainage some 15 km. north of Cuilapa. I do not know what conditions obtain there. Miller collected there. Elevation, probably about 900 m. Not on Map 2.

Soledad Grande. — A hamlet on the Soledad Grande block 48 km. east of Guatemala. The highland mass upon which it is situated may be a part of the Las Nubes block to the west from which it appears to have been separated by the development of a *graben* in which lies the village of Matequescuintla. Soledad Grande is situated on the rolling highlands which are utilized primarily for grazing, lumbering, and a little agriculture. Though much of the virgin forest has been cut, there are still some fine stands of temperate broadleaf forest and groves of pine and oak in the area. Though there is little surface water in the region, heavy night dews and fog render the high surface fairly humid. The village of Miramundo is the main center of this region and lies only 5 km. west of Soledad Grande, misplaced on the Geographical Society map, on which it is shown west of Matequescuintla instead of east. I collected between elevations of 2300 m. and 2525 m. Elevation, 2515 m.; March 19-21.

Volcán Jalapa (Volcán Jumay). — One of the volcanic cones characteristic of the landscape of the southeast. Though entirely cultivated to 2000 m. most of the crest is still in virgin broadleaf forest. Cutting, however, has begun on the crest. The forest is wet, and a fine mulch layer covers the ground. I studied the volcano from my base at San Lorenzo. Elevation (crest), 2120 m.

APPENDIX II. ANNOTATED LIST OF SPECIES

As early as 1944 I had reconnoitered southeastern Guatemala, but owing to restrictions on arms and difficulties of travel during that war year, I was able to collect a mere handful of specimens. In 1945 and again in 1947 the Fish and Wildlife Service of the United States Department of the Interior conducted a fish and wildlife survey of Guatemala (Saunders, Holloway, and Handley, 1950) during the course of which Robert R. Miller, then of the United States National Museum, collected a few reptiles and amphibians from the southeast. These are preserved in the collections of the U. S. National Museum. Richard E. Tashian, at the time a student at Purdue University, studied the avifauna of a part of the region in 1950-51 and such reptiles and amphibians as he secured during the course of his investigations were turned over to the Museum of Zoology, University of Michigan. In 1951 Luis de la Torre, now affiliated with the Chicago Natural History Museum, secured a few specimens in the southeast, and these were also presented to the Museum of Zoology. Again in 1952 Mr. de la Torre, collecting for the Chicago Natural History Museum but traveling with me, made a small but important collection of amphibians and reptiles which are in the Chicago Natural History Museum collection. The bulk of the material upon which this report is based, however, was collected by me in 1952. I have had access to roughly 1300 specimens (tadpoles counted by lots) divided among 59 forms, all of which are familiar to me in the field. In the following section all forms, unless otherwise indicated, are in the collections of the Museum of Zoology, University of Michigan. USNM refers to material in the U.S. National Museum and CNHM to that in the Chicago Natural History Museum. The designation LCS refers to my own field numbers and represents material which will eventually be turned over to the Museum of Zoology. Table II is a systematic breakdown of the collections I have examined and represents, I believe, a complete list of all amphibian and reptilian material that is known from the Southeastern Highlands.

TABLE II

Herpetological material available for study from southeastern Guatemala

Group	Genera	Forms	Specimens
Caudata	3	3	39
Salientia	9	23	655
Chelonia	1	1	4
Sauria	12	20	523
Serpentes	11	12	39
Totals	36	59	1260

Oedipina taylori Stuart

Jutiapa, No. 98125, mentioned in type description (Stuart, 1952: 3) but not designated a paratype.

No further specimens of this species have been secured from the Southeastern Highlands. Mertens (1952: 21) has indicated that four specimens of *Oedipina salvadorensis* Rand collected by him in the vicinity of the type locality of that species are very similar to *taylori*. It is my opinion that *salvadorensis* will prove to be a synonym of *taylori*.

This is one of the species that suggests faunal affinities between the Jutiapa region and the Pacific versant.

Pseudoeurycea exspectata Stuart

Soledad Grande (Miramundo), Nos. 107999 (holotype), 106762 (16), all paratypes, LCS 5367 (eggs), CNHM Nos. 68730-49, 68750 (eggs).

This is one of the species that indicates faunal affinity between the Southeastern Highlands and the higher Southwestern Highlands to the north and west. It is a ground form in the wet, broadleaf forests above 2000 m. Such habitats are extremely rare in the southeast and probably do not occur east of Jalapa. More detailed notes on this species are in the original description (Stuart, 1954: 159-61).

Magnadigita sp.

Soledad Grande, CNHM No. 68729.

A single juvenile 25 mm. in body length was secured from a bromeliad together with some of the paratypes of *Pseudoeurycea exspectata* by De la Torre. That the individual belongs to some species, either described or undescribed, in the *dunni* group (Stuart, 1952) seems fairly obvious.

The specimen is geographically closest to *Magnadigita engelhardti* (Schmidt) from intermediate elevations of the Pacific versant. It may be pertinent to note that *Pseudoeurycea exspectata*, with which it was secured, is apparently genetically closest to *Pseudoeurycea goebeli* (Schmidt), also of the Pacific versant of Guatemala.

It is not improbable that the species is restricted to elevations above ca. 2000 m., in which case it is to be expected only in the northwestern part of the southeast.

Bufo coccifer Cope

Esquipulas, Nos. 106809 (16), 106810 (4), 106811 (32), 106812 (12); Jalapa, Nos. 106813 (29), 106814 (11).

In a recent paper (Stuart, 1954: 164-65) I noted that the Jalapa population of *coccifer* is slightly atypical, especially as regards size. Further investigation may reveal that the Jalapa population represents intergrades between *coccifer* and the recently described *ibarrai.*

In my field notes I noted that the ground color of the species varies from light yellowish brown to dark brown and that the darker markings vary from dark brown to reddish brown. The underparts are yellowish white and the narrow, light, middorsal line is light yellow. The chin of males is lemon-yellow, and the parotoids vary from bright yellow to orange-red.

The range of *coccifer* on the Southeastern Highlands is very imperfectly known. It was surprising not to find it in the Jutiapa region, considering the fact that Mertens reported it from El Salvador (1952: 25). I suspect that the species had already bred and retired for the year by the time I arrived at that locality for my wet-season studies. At both Esquipulas and Jalapa the species was abundant early in the wet season. It breeds in temporary ponds in open pasture or grasslands. It was surprising to find so few females, only six of this sex having been secured at the two localities. By mid-June, though the males were chorusing at Jalapa, I found neither tadpoles nor eggs of the species. The form probably does not occur at elevations above ca. 1500 m. in Guatemala, and I have never secured it on the lowlands. Mertens, however, gave its vertical limits in El Salvador as from the coastal plain to 2000 m. (1952: 25), and Carr (1950: 580) reported it from the cloud forest of Honduras. That environment is certainly very different from the dry-lands of southeastern Guatemala. I should not care to hazard a guess as to why there should be such differences in its environment in different parts of its extensive range.

Bufo ibarrai Stuart

San Lorenzo, Nos. 108000 (holotype), 106806 (10), 106807 (3, all paratypes), and CNHM 68711 (paratype).

This species probably replaces *Bufo coccifer* at elevations above 1500 m. on the Southeastern Highlands. The highest record is that of the type series, 1725 m., and the lowest is 1000 m. in the Salamá Basin to the north (*Bufo microtus* of Schmidt and Stuart, 1941: 238).

The species may be an early breeder. I base this assumption on the fact that at San Lorenzo in mid-June the majority of the individuals were taken singly or in groups of two or three in wet meadows or in small water holes, but there was no chorus of the form. Furthermore, in the Sierra de las Minas only a few days after I had left San Lorenzo *Bufo* tadpoles were secured. It seems quite probable that these tadpoles were those of *ibarrai*, inasmuch as no other *Bufo* was taken at that locality.

I cannot be certain that the tadpoles of *ibarrai* can be distinguished from those of other Guatemalan species of *Bufo* which are all much alike (with the exception of *Bufo bocourti*). It may be noted, however that the *ibarrai* tadpoles (if such they are), have a much shorter outer tooth row than I have observed in the tadpoles of other species of the genus. They are, furthermore, much lighter than those of, for instance, *Bufo marinus*. This feature is especially noticeable on the fore part of the ventrum.

Bufo luetkeni Boulenger

Jutiapa, Nos. 106795 (3); Santa Catarina, No. 106796.

Described from three specimens, the four individuals taken by me are the first to be recorded, to my knowledge at least, since the type description; these were secured some 750 air-line km. from the type locality. I believe, however, that there may well be other specimens languishing in collections under other names. Certainly, this seems to be the case in at least one instance—Mertens' photograph of a *Bufo valliceps* (Mertens, 1952: Taf. 9, Fig. 43). I think that there can be little doubt that *Bufo luetkeni* (as used here) is figured in this case. The species could well be confused with *valliceps* (I did so in the field) from which it differs mainly in the shape and size of the parotoid glands.

My specimens match the description of the types reasonably well. The snouts of my specimens are more pointed than rounded, as described by Boulenger. The tympanum in the females is as described, but is comparatively smaller in my single male. The first fingers are considerably longer than the second in the females, as noted in the types, but the difference in the lengths is less pronounced in the male. I judge the toes to be somewhat less fully webbed than noted by Boulenger. The lateral row of spines noted by Günther (1901: 253) is just barely evident in four out of eight sides in my series. Aside from these differences, all of which may either vary with sex or which may require subjective treatment, the four specimens from the Southeastern Highlands are in accord with the descriptions of Boulenger and Günther.

The most characteristic feature of the species is its ridiculously small parotoid glands, which are oval in outline. From *valliceps* they may readily be differentiated by the smaller parotoids, lesser development of the row of lateral spines, and somewhat larger size; my male has a head-body length of 91.3 mm., and the smallest of the three females, 84.5 mm. I know of nothing in northern Middle America to which this species shows any close genetic affinity, and I am not well enough acquainted with more southern bufos to suggest relationships in that direction.

The species apparently barely enters the southeast from the Pacific versant. All specimens were taken during the dry season following brief showers, and all were secured in the immediate vicinity of running water. This would suggest that the form may be a lotic species, which may well account for its scarcity in collections.

Bufo marinus (Linnaeus)

Esquipulas, Nos. 106800-01, 106803, LCS 5248 and 5308 (tadpoles); Jalapa, Nos. 98110, 106802; Laguna de Atescatempa, USNM Nos. 123618-19; Jutiapa, Nos. 106804 (5), 106805 (10), LCS 5387 (tadpoles); Río Mita [? Ostúa] (north of Mongoy), USNM 123620 (tadpoles); Sanarate, USNM Nos. 123660, 123661 (17 juveniles); Santa Catarina, No. 106798.

This species was common and widely distributed over the Southeastern Highlands to 1400 m. elevations. Tadpoles of this species occurred in tremendous numbers in quiet pools of the larger streams in the Esquipulas area in mid-March.

Bufo valliceps Wiegmann

Esquipulas, No. 106794 (5).

This species occurs only sparingly on the eastern edge of the Southeastern Highlands and then only at elevations below 1000 m.

Engystomops pustulosus (Cope)

Esquipulas, No. 106776 (52); Jalapa, No. 106775 (8); Jutiapa, No. 98107 (3), 106774 (5).

Like most of the other lowland amphibians, this species is widely distributed over the Southeastern Highlands. It is one of the earliest breeders, and its frothy nests are abundant, especially in small puddles which many frogs seem to avoid, soon after the rains begin. It was surprising to find this species at almost 1400 m. in the Jalapa region, as I had not encountered it previous to 1952 above ca. 500 m. in Guatemala.

Leptodactylus labialis (Cope)

Esquipulas, No. 106771 (2); Jalapa, No. 106772 (2); Jutiapa, No. 106773.

This widespread lowland species apparently attains its upper limit in Guatemala at some 1400 m. (Jalapa). Both this and the following species are more common on the Southeastern Highlands than collected specimens would indicate. The habit of calling from small excavations in the sod renders difficult the collecting of *Leptodactylus*, and *labialis* is especially difficult to locate since, unlike *Leptodactylus melanonotus*, it does not occur in streams where it might be secured during the dry season. Five of the above specimens are females that were hopping about in light cover where rain pools had formed. A female collected at Jutiapa on July 8 had not yet deposited its eggs.

Leptodactylus melanonotus (Hallowell)

Esquipulas, No. 106770 (5); Jalapa, No. 106767; Jutiapa, Nos. 98106, 106766 (2), 106769; Laguna del Pino, USNM No. 123649; Mongoy, No. 106766.

In the dry season this species was secured from beneath rocks in permanent streams, and a female collected in late March at Jutiapa was distended with fully formed eggs. With the onset of the rains it appears to leave such permanent waters and to move to higher ground. In open meadows with scattered rain pools the males were frequently heard calling from the nests they had excavated beneath clumps of sod or by low shrubs; the females were secured while they were hopping about in the open. A female collected at Jalapa in early June had not yet deposited its eggs, though the rains had "broken" some three weeks previously. It was somewhat surprising to find this form, as well as the preceding one, as high as 1400 m. (Jalapa).

Eleutherodactylus rugulosus (Cope)

Esquipulas, No. 106765.

I am at a loss to explain the absence of this species from the greater portion of the Southeastern Highlands in view of its occurrence up to 1800 m. in other parts of Guatemala. True, much of the terrain of the Southeastern Highlands is unsuited to the species, but in riparian forests it seems that the form would find a favorable environment. The fact that the species is not one that is easily overlooked—my experience has been that it occurs in moderate abundance wherever it is present—leads me to believe that it and other eleutherodactylids are not members of the Southeastern Highland herpetofauna proper. The single specimen collected was taken in the mulch of a coffee grove near a small stream at Esquipulas.

Hyla baudini Duméril and Bibron

Esquipulas, No. 106799 (28); Jalapa, No. 106792 (11); Jutiapa, No. 106789; Santa Catarina, No. 106790.

This wide-ranging form is apparently generally distributed over the Southeastern Highlands up to about 1400 m. elevation. The specimens from Jalapa at 1400 m. were at the highest level that I have ever before encountered the species in Guatemala. Failure to observe more specimens at Jutiapa was undoubtedly owing to the late date at which I visited the locality for wet-season studies. A pool on the outskirts of the village was literally alive with the tadpoles of this species, and it was indicated that the form had completed its breeding activities about three weeks before my arrival.

Hyla microcephala martini Smith

Esquipulas, No. 106844.

This name is utilized only tentatively for what has been known as *Hyla underwoodi* Boulenger (see Smith, 1951: 187). Not more than a dozen individuals were heard calling, and these were all from bushes overhanging steep-sided water holes, thus making them extremely difficult to collect. I am familiar with this early breeder at lower elevations and am accustomed to find it in great numbers early in the rainy season. Its small population at Esquipulas I interpret as indicative of its having approached the upper limits of its vertical distribution. It apparently enters the Southeastern Highlands only along their eastern fringe.

Hyla robertmertensi Taylor

Jutiapa, No. 106845.

This Pacific representative of the *Hyla microcephala* group was heard only once on the Southeastern Highlands, when the above specimen was found singing from a bush overhanging a water hole in the dense second growth. Because I collected at Jutiapa late in the amphibian breeding season, it is impossible to say whether or not this species occurs only sparingly at higher elevations, as appears to be the case with *Hyla microcephala martini.* About 1000 m. elevation appears to be its upper limit.

Hyla staufferi Cope

Esquipulas, Nos. 106784 (4), 106785 (15); Jalapa, No. 106788 (44); Jutiapa, No. 106786 (2).

This species is apparently widely distributed over the Southeastern Highlands at elevations below 1500 m. It was surprising to find it so common at Jalapa, which is some 400 m. higher than I had ever before collected it in Guatemala. During the dry season the species was found beneath the leaf sheaths of bananas. Once the rains begin *Hyla staufferi* commences its breeding activities by calling in the trees, and I even heard it singing from oak trees at midday in the Esquipulas region. At that locality it was heard in trees at the time of the first rains (May 20); three specimens were found in low bushes or on the ground on the nights of May 22 and 23, but it was not until May 27 that it was chorusing in any numbers in pools. By June 8 the species had apparently reached the peak of its breeding activities at Jalapa, and by July 8 it had all but completed its activities at Jutiapa.

Hyla walkeri Stuart

San Lorenzo, Nos. 106817 (holotype), 106815-16, 106818-19 (all paratypes).

This form is apparently restricted to intermediate elevations on the Southeastern Highlands. Notes on its natural history and affinities are included in the original description (Stuart, 1954: 165-69).

Ptychohyla spinipollex (Schmidt)

San Lorenzo, No. LCS 5009 (tadpoles).

Though no adults of this species were secured, there can be no question as to the identity of the very distinctive tadpoles (Stuart, 1948: 32-34, Figs. 5-6) which were taken from pools in a nearly dry freshet in early February. Associated with these tadpoles were those of *Rana macroglossa* and *Plectrohyla guatemalensis*. The species is probably restricted to intermediate elevations in the northern and eastern portions of the southeast.

Plectrohyla cotzicensis Stuart

Soledad Grande, CNHM Nos. 68716-20, 68722-27.

Of the above specimens only one, a female with eggs, is an adult. The remainder are either half-grown or juveniles not much beyond metamorphosis. In all the tarsal folds are rather weakly developed as compared with strong development, even in juveniles, stemming from the Sierra Madre (vicinity of the type locality). In other respects the series seems to be typical.

All the above specimens were collected by Luis de la Torre in a bromeliad in early April at roughly 2500 m. elevation. This is the first record of the species inhabiting bromeliads and is also the lowest elevation at which the species has been found. The form is, of course, a Southwestern Highlander that apparently has invaded the Southeastern Highlands only at higher elevations in their western section.

Plectrohyla guatemalensis Brocchi

Las Nubes, Nos. 100520, 100522 (both tadpoles); San Lorenzo, Nos. 106782 (3), LCS 5009 (tadpoles); Soledad Grande, LCS 5338 (tadpoles); CNHM No. 68721.

The Soledad Grande specimen, collected by Luis de la Torre, was found at the same elevation as *Plectrohyla cotzicensis*, and I found the tadpoles of the species common several hundred meters lower. This is the first record of *P. guatemalensis* and *P. cotzicensis* occurring together. It is quite probable that the two occupy different breeding sites, the former in larger streams and the latter in tiny *riachuelos*. At San Lorenzo I found in mid-February three subadult specimens in a bromeliad on a tree overhanging a nearly dry stream from which I secured tadpoles of this species, and in early May (1949) I took other tadpoles together with those of *P. matudai* from small streams on the Las Nubes block.

Inasmuch as *P. guatemalensis* is widely distributed throughout the oak-pine zone of Guatemala from about 1500 to 2500 m., I should not be surprised to find it in any suitable habitat throughout the Southeastern Highlands as well as in adjacent Honduras. The species has recently been reported from El Salvador (Mertens, 1952: 31), in the pine zone.

Plectrohyla matudai Hartweg

Las Nubes, Nos. 100521, 100523 (both tadpoles).

This is the first record of the species from other than the slopes of the Pacific side of Guatemala and Mexico, and indicates that the Pacific versant element apparently just barely enters the Southeastern Highlands at elevations of about 2000 m. in their western section. The stream from which the tadpoles were taken is in the Pacific drainage. Although tadpoles without adults are generally inconclusive evidence for the presence of a species, there can be no mistaking the tadpole of this species, which has the fanglike projections on its back..

Hypopachus barberi Schmidt

Guatemala City, No. 106777; San Lorenzo, No. 106778 (3), LCS 6211 (tadpoles).

This species is the common *Hypopachus* of the Southwestern Highlands in the oak-pine zone. In occurring in a similar environment on the Southeastern Highlands with *Pseudoeurycea*, several species of *Plectrohyla*, and *Sceloporus malachiticus smaragdinus*, it is one of the indicators of faunal affinity between the higher western parts of the Southeastern Highlands and the uplands to the north and west.

Though San Lorenzo lies in close proximity to Jalapa, it is over 300 m. higher. At the latter only *Hypopachus championi* Stuart was secured, and in abundance, while at San Lorenzo I found only *Hypopachus barberi*. Thus, it is indicated that *barberi* is unquestionably the common *Hypopachus* of the plateau above ca. 1500 m. This conclusion is strengthened by the fact that at Guatemala City (roughly 1475 m. elevation) I collected the two forms in the same rain pond near the southern outskirts of the city. It was unfortunate that I did not have an opportunity to work other areas of the Southeastern Highlands at approximately this same elevation in order to gain some understanding of the ecological relationships of the two. To my knowledge this is the first time that two species of this genus have ever been taken together.

Tadpoles of the species were secured at San Lorenzo in a small, quiet, temporary stream flowing through a grassy basin that at the time was completely covered with several inches of water.

Hypopachus championi Stuart

Esquipulas, No. 106779 (15); Guatemala City, No. 107091; Jalapa, Nos. 106780 (42), 106781 (16).

At one time I believed that a simple upland (*inguinalis*) group of *Hypopachus* could be readily differentiated from a lowland (*cuneus*) group on the basis both of the shape of the inner metatarsal tubercle and of the mouth parts of the tadpoles (Stuart, 1951: 54). I now believe that it may eventually be necessary to recognize at least three groups, viz., the highland *inguinalis* group, a lowland *cuneus* group, and a third group which at the present is not well defined either with respect to its morphological characters or to its content. One thing seems fairly certain, *championi* of central and southeastern Guatemala and *Hypopachus maculatus* Taylor of interior Chiapas are closely related (Stuart, 1954: 13), and neither can be assigned to either the *inguinalis* or *cuneus* group. It is entirely possible that they will connect with some of the Mexican forms of the Pacific versant, but these are still too poorly known to demonstrate such a possibility.

It is indicated that *championi* replaces the *inguinalis* group below about 1500 m., while *cuneus* occurs at even lower elevations and is, in fact, unknown above ca. 500 m. It is possible that *championi* and its relatives may prove to be more of a xeric type than either of the other two groups.

This species apparently is an early pond breeder, though not so early as *Engystomops* or *Hyla baudini*. It is impossible to say how extensively this form is distributed over the Southeastern Highlands. It is known from the northern and eastern sections, but is as yet unknown from the southwestern. Were it present in the Jutiapa region, however, it seems that tadpoles should have been secured when I visited the village in early July, as an abundance of suitable breeding ponds occur in the vicinity.

Rana macroglossa Brocchi

El Carnero, CNHM No. 68728 (tadpoles); El Rosario, USNM No. 123612 (tadpoles); Esquipulas, Nos. 106822, LCS 5230-31, 5243 (tadpoles); Jutiapa, Nos. 106824 (2), LCS 5387, 5401 (tadpoles); Laguna de Ayarza, USNM Nos. 125349-400 (juv.), 125401 (tadpoles); Laguna del Pino and vicinity, USNM Nos. 123613 and 123648 (both tadpoles), 123658; Los Ocales, Nos. 100507, 100524-25 (tadpoles); Río Atulapa, USNM No. 125339 (tadpoles); Río La Paz, USNM Nos. 123617 and 125326 (both tadpoles); San Lorenzo, Nos. 106825 (15), 106826, LCS 5009-10 (tadpoles); San Pedro Pinula, USNM No. 125323 (tadpoles); Santa Rosa, USNM Nos. 123614-16 (all tadpoles); vicinity of Guatemala City, USNM Nos. 123601-02 (tadpoles), 126303, 123640-46, 123647 (tadpoles), 125320-21, 125322 (tadpoles).

This and the following species appear to be essentially running-water types, but with some rather distinct differences in the nature of their habitats. *Rana palmipes* in northern Central America is a lowlander that lives in the larger streams and rivers, especially those in which deep pools occur intermixed with riffles. *Rana macroglossa,* in contrast, is an uplander that inhabits headwater brooks with considerably greater velocity than those in which *Rana palmipes* is present.

Rana macroglossa is widely distributed over the Southeastern Highlands to at least 2000 m., and its tadpoles may be found in any brook at almost any season of the year. It may, in fact, be heard calling throughout the year, especially in the evenings and on cloudy days. It is, however, rather difficult to secure, for it lies beneath rocks in streams and when disturbed swims rapidly away with the current.

Rana palmipes Spix

Esquipulas, No. 106827.

Apparently, most of the Southeastern Highlands are above the vertical limits of this typically lowland ranid. It is not a species that is easily overlooked, even though its normal habitat is in and along larger streams. Finding it at 910 m. constitutes, in fact, the highest elevation at which I have taken the species in Guatemala. The single specimen was taken from a shallow, sluggish, ditchlike stream in the Esquipulas Valley. In the same stream *Rana pipiens* was abundant.

Rana pipiens Schreber

Esquipulas, Nos. 106836-37, 106838 (5), 106839 (3), 106840 (11); Jalapa, Nos. 106828 (11), 106829 (11), 106830 (10); Jutiapa, Nos. 106831-33, 106834 (5), 106835 (14); Los Ocales, Nos. 100506 (2), 100526 (tadpoles); San Lorenzo, No. 106843; Santa Catarina, No. 106842; vicinity of Guatemala City, USNM Nos. 123642, 123647 (tadpoles).

I found this species widely distributed over the Southeastern Highlands up to about 2000 m., but it undoubtedly goes higher and, where pools are available, it probably occurs at the very highest elevations encountered in the southeast. The species is active throughout the year, and during the dry season, as some pools dry up, very large populations occur in ponds that retain water through the long drought period.

Phyllodactylus eduardofischeri Mertens

Finca El Carnero, Nos. 106556-57, CNHM 68621-22; Finca Mongoy, No. 106863.

The above specimens closely match Mertens' recently described form, and on geographic grounds it would be expected that the Salvadoran and Pacific Guatemalan populations would be conspecific. These more southern populations (I have seen specimens from as far south as Nicaragua) are quite different from those from the vicinity of Tehuantepec in which the scales on the upper surface of the head are very much smaller.

The form probably is restricted to elevations below 1200 m. The El Carnero specimens were secured by Luis de la Torre from a small cave which he had entered in search of bats. The Mongoy specimen was taken on the wall of an outbuilding at night. All of the specimens either lack tails or have regenerated ones.

Sphaerodactylus glaucus glaucus Cope

Esquipulas, Nos. 106864-66.

This little gekko is a typical representative of the Caribbean lowland fauna. It is well known to the inhabitants of Esquipulas, where it is not uncommon in the houses. It is one of a group of forms which, having attained a pass (Río Lempa) across the Southeastern Highlands, have nevertheless not spread to the Pacific lowlands.

Anolis crassulus crassulus Cope

Las Nubes, No. 100501; Los Ocales, No. 100500 (6); San Lorenzo, CNHM No. 68692; Soledad Grande, CNHM Nos. 68693-94.

This form, a typical Southwestern Highland element, enters the Southeastern Highlands only in their eastern section, and here only at high elevations. The San Lorenzo individual was taken on Volcán Jalapa, the only terrain east of Soledad Grande high enough to provide a suitable habitat for the species.

Anolis sericeus Hallowell

Esquipulas, Nos. 106947, 106948 (2), 106949; Jutiapa, Nos. 106950 (3), 106951 (2), CNHM No. 68695; Santa Catarina, No. 106952 (2).

In a forthcoming paper I shall treat variation in *Anolis sericeus* (auct.) at some length. It can be shown that several populations, especially those of the Caribbean and Pacific versants of Central America, might be accorded taxonomic recognition. It is sufficient to note here that, as might be expected, material from the Jutiapa region falls in line with the Pacific population, whereas the Esquipulas specimens are typical of the Caribbean population.

I did not find this species above the 1000 m. contour. Though observed in rock walls far removed from water, the species was most common in riparian environments in the southeast.

Anolis tropidonotus Peters

Esquipulas, Nos. 106957 (2), 106958 (3).

This species, typical of the Caribbean lowlands, occurred sparingly in the riparian forest and in coffee and banana groves along the headwater streams of the Río Lempa. It is surprising that this species, having attained a suitable environment that from Esquipulas is continuous to the Pacific versant, has apparently not managed to invade the latter region. In this respect it parallels the condition noted of *Sphaerodactylus g. glaucus*.

Basiliscus vittatus Wiegmann

El Rosario, CNHM No. 68618; Esquipulas, Nos. 106939-41; Jalapa, No. 106934; Jutiapa, Nos. 106937 (2), 106938; Mongoy, No. 106932; San Pedro Pinula, No. 106936; Santa Catarina, No. 106933.

As was to be expected, *Basiliscus* proved to be the common riparian lizard of lower elevations on the Southeastern Highlands. Though one specimen was secured at almost 1400 m. (Jalapa), the species was rare above 1000 m.

Sceloporus lunaei Bocourt

El Carnero, CNHM Nos. 68623-31; El Rosario, CNHM Nos. 6843-52; Esquipulas, Nos. 106867-69, 106870 (3), 106871 (5), 106872 (15); Jalapa, No. 106873 (6); Jutiapa, No. 106881 (17); Las Nubes, Nos. 107540-41; San Lorenzo, Nos. 106879, 106880 (17).

Mertens (1952: 48-51, Taf. 5, Figs. 18-20, Taf. 12, Figs. 69-70) has commented at length on *Sceloporus m. malachiticus* Cope in El Salvador and contrasted his specimens with typical *Sceloporus acanthinus.* Judging from his figures I should say that at least a part of his Salvadoran series is *lunaei,* and this species, heretofore known only from central Guatemala, very probably ranges southward into both Honduras and El Salvador. In a forthcoming paper I shall present a systematic consideration of the form.

On the Southeastern Highlands *lunaei* was found to be the common lizard of the oak-pine zone between elevations of 900 and 2200 m. The species occurs most frequently in rocky habitats in oak groves and is particularly common in rock walls in forested areas. In the Jutiapa region I did not encounter it in grassland areas, and it was not until I visited the oak forests well to the west of the village at Acatempa that I noted it in this region. Along the Pacific slopes of the Southeastern Highlands I have never found it below 1000 m.

Sceloporus malachiticus smaragdinus Bocourt

Las Nubes, No. 107541; Los Ocales, Nos. 100492-93; Santa Lucia, CNHM Nos. 68653-54; Soledad Grande, Nos. 106882 (5), 106883 (8), CNHM 68632-42.

In a previous paper (Stuart, 1951: 56-57) I reported that this species was secured on the higher blocks just southeast of Guatemala City but that on the Las Nubes block farther to the east the typical form was secured. A further study of this material reveals that this conclusion was incorrect. What I had previously referred to as the typical form proves to be *Sceloporus lunaei,* and it is now apparent that the typical form of *Sceloporus malachiticus* does not occur in Guatemala.

It seems that *Sceloporus m. smaragdinus* and *Sceloporus lunaei* come in contact with each other at about the 2000 m. contour. Though the former descends to 1500 m. in northwestern Guatemala, I have not found it below 2000 m. in the southeast. It was surprising not to find it on Volcán Jumay (2150 m.), where only *lunaei* was taken. This could indicate that Jumay, an isolated peak surrounded by terrain that lies at the 1500 m. level, is of fairly recent origin. It is not unreasonable to suspect that during the height of Wisconsin glaciation *Sceloporus malachiticus* very probably descended to much lower levels than at present, in which case it would have had an opportunity to reach Jumay had it then been in existence.

Sceloporus m. smaragdinus was the commonest lizard on the Soledad Grande block,where it abounded along wooden fences, around the houses, and on the stumps of large pines and cypresses that had been cut several years previously.

Sceloporus squamosus Bocourt

Esquipulas, Nos. 106899 (5), 106900 (2), 106901, 106902 (3), 106903, 106904 (6); Jutiapa, Nos. 106893-95, 106896 (7), 106897 (3), 106898 (2); Mongoy, Nos. 106891 (2), 106892 (8); San Pedro Pinula, No. 106887; Santa Catarina, No. 106888.

Not until the southern edges of the Southeastern Highlands are approached does this species outnumber *Sceloporus variabilis olloporus*. Throughout the dry Motagua Valley and in the drier portions of the eastern part of the Southeastern Highlands the latter species is far more common than *squamosus*. The fact that *squamosus* descends onto the Pacific coastal plain and ranges north into eastern Chiapas, a region in which *olloporus* is unknown, suggests that the former is far more tolerant to mesic conditions than is the latter.

Where the two species occur together I have been unable to find any differences in their habitats, and I have on occasion found the two sharing the same large boulder. Though *squamosus* ascends to 1500 m. on the Pacific versant, I did not find it above 1300 m. on the Southeastern Highlands, at which elevation it was extremely rare.

Like *variabilis olloporus, squamosus* is a typical example of a form that, having attained the dry basins and valleys of middle Guatemala from southern Mexico, has crossed the Southeastern Highlands to reach the Pacific versant.

Sceloporus variabilis olloporus Smith

El Carnero, CNHM Nos. 68655-68; Esquipulas, Nos. 106909 (5), 106910 (7), 106911 (9), 106912 (2), 106913 (5), 106914 (5), 106915 (9), 106916 (6), 106917 (17); Jutiapa, No. 106906; Mongoy, Nos. 106926 (2), 106927; San Pedro Pinula, No. 106907; Santa Catarina Mita, Nos. 106924 (2), 106925 (12).

This form finds its closest genetic affinity in the typical form which inhabits Mexico and the headwater valleys of the Río Grijalva in Guatemala and is another example of a reptile that has crossed the Southeastern Highlands to reach the Pacific versant and has moved as far south as Costa Rica. Only in the drier portions of Guatemala and Honduras does it appear on the Caribbean side of Central America. Between the Isthmus of Tehuantepec and central El Salvador no representative of the *variabilis* group is known from the Pacific versant. In a previous paper (Stuart, 1954: esp. pp. 15-16, Map 4) I have discussed the matter at length.

Though I have collected specimens up to 2200 m. on the Southwestern Highlands of Guatemala, I did not encounter it above 1100 m. in the southeast. A juvenile was taken on May 19, only a few days after the rainy season had begun in 1952.

Ctenosaura similis (Gray)

Mongoy, No. 106945; Santa Catarina, No. 106946.

Though common in the Motagua Valley and in some of the lower headwater valleys that drain into Lago de Güija, this wide-ranging species apparently is unable to cope with even the lower elevations that cut across the Southeastern Highlands. Unless the species crosses the Central American isthmus farther south, the only link between the Caribbean and Pacific populations is in the Isthmus of Tehuantepec region.

Barisia moreleti fulva (Bocourt)

Soledad Grande, No. 106861, CNHM No. 68615.

Though single individuals of this genus are often difficult to assign to any subspecies, the above specimens are quite typical of *fulva* in all their characters. The individuals certainly lack the speckled pattern that appears to be characteristic of *salvadorensis* (Mertens, 1952: 53, Taf. 11, Fig. 62).

The Museum of Zoology specimen was found beneath a log in a corn field at 2500 m. elevation. The lizard is well known to inhabitants of the region. Reports of a slow-moving arboreal lizard in the same area leads me to believe that some form of *Abronia* may also occur on the Soledad Grande highlands. Both gerrhonotids are considered venomous locally.

Gymnophthalmus speciosus birdi Stuart

Esquipulas, Nos. 106847-48.

Mertens has recently described not wholly unexpected intergrades between *birdi* and *speciosus* (1952: 56-57, Taf. 13, Fig. 78). The above specimens, however, are typical *birdi*, and it seems fairly certain that this genus, almost restricted to the Pacific slopes of Central America, has utilized the Southeastern Highlands in crossing over to the Caribbean versant to invade the dry lands of central Guatemala.

Though only two specimens were collected at Esquipulas, others were seen, and the species is probably not uncommon in the oak groves of the Esquipulas basin. I did not encounter it in any other part of the Southeastern Highlands.

Ameiva undulata hartwegi Smith

El Carnero, CNHM Nos. 68696-702; Esquipulas, Nos. 107007 (2), 107008 (2), 107009 (2), 107019; Jutiapa, Nos. 106996, 106997 (5), 106998, 106999 (18); Mongoy, Nos. 107002 (6), 107003, 107004 (4); San Pedro Pinula, Nos. 107011, 107012 (2); Santa Catarina, No. 107006 (11).

Only the populations from the eastern and northern parts (Esquipulas and San Pedro Pinula) of the highlands can be considered typical *hartwegi*. Material from Jutiapa, Mongoy, El Carnero, and Santa Catarina, all in the Pacific drainage, show definite *parva* influence. Yet regarded as a whole these populations are definitely closer to *hartwegi* than to *parva*. The problem of *hartwegi-parva* intergradation will be discussed under *parva*.

On the Southeastern Highlands I found *Ameiva u. hartwegi* only in heavily shaded areas, which in this region means riparian forests. Though I have secured the form as high as 1500 m. in other parts of Guatemala, it did not occur above 1100 m. on the Southeastern Highlands.

Ameiva undulata parva Barbour and Noble

El Rosario, CNHM Nos. 68708-10; Las Viñas, Nos. 107073-74.

Only the El Rosario specimens are typical *parva*, while those from Las Viñas retain some *hartwegi* features. It is not improbable that all the above specimens are merely a portion of an intergrading population, a suggestion that warrants consideration inasmuch as El Rosario and Las Viñas are but a few kilometers apart.

It has been noted that in the southwestern parts of the Southeastern Highlands *hartwegi* shows some *parva* influence. In the northwestern parts of the highlands, however, we are dealing with *parva* that shows some *hartwegi* influence. Certainly, the whole problem of intergradation between these two forms cannot be settled on the basis of material now available. If the Jutiapa-Mongoy-Santa Catarina materials, all of which stem from Pacific versant drainage systems and lie within a radius of less than 15 km., are combined, 31 specimens may be definitely assigned to *hartwegi*, 4 to *parva*, and 11 may be considered intergrades. In dealing with populations from El Salvador Mertens (1952: 54) presented data that suggest that at least certain individuals of what he called *parva* show some *hartwegi* influence. Unfortunately, he gave no data on individual specimens nor did he make any geographic correlations to indicate either the position or degree of possible intergradation. In the five specimens from Las Viñas and El Rosario two from the former are definitely intergrades and three from the latter seem to be typical *parva*. The Jutiapa-Mongoy-Santa Catarina specimens are somewhat farther removed from the Pacific versant proper (and hence true *parva*) than are the Las Viñas-El Rosario specimens. At Finca La Gloria on the Pacific slopes of the Southeastern Highlands and east of Jutiapa only true *parva* was secured in 1949. From these scattered data it is suggested that intergradation between *parva* and *hartwegi* may be expected within the limits of a band possibly 20 km. in width along the entire western (Pacific) section of the Southeastern Highlands.

Like *hartwegi*, this form is essentially a riparian forest inhabitant.

Cnemidophorus deppi deppi Wiegmann

Mongoy, Nos. 106987 (11), 106988 (8), 106989 (6), 106990 (7); Santa Catarina, No. 106991 (10).

This form is a typical lowlander. I have never secured it above 900 m. in Guatemala, and on the Southeastern Highlands it did not seem to range above 700 m. It is, furthermore, a characteristic species in all dry-land environments. South of the Isthmus of Tehuantepec it has much the same range as *Sceloporus v. olloporus* with the exception that it is more extensively distributed along the Pacific versant, though it is unknown whether or not there is continuity in its range along the very wet coastal plain of eastern Chiapas and western Guatemala. If the species is continuous in its distribution across the Southeastern Highlands, continuity could occur only along the line from Ipala to the region of Agua Blanca, where elevations are sufficiently low to fall within the vertical limits of the species.

Cnemidophorus sacki motaguae Sackett

El Carnero, CNHM No. 68691; Jutiapa, Nos. 106965 (11), 106966 (4), 106967, 106968 (10), 106969 (7), 106970 (5), 106971 (2), 106972; Mongoy, Nos. 106973 (2), 106974, 106975 (6), 106976; San Pedro Pinula, Nos. 106962 (5), 106963 (7), 106964 (8); Santa Catarina, Nos. 106977 (4), 106978 (7).

I have elsewhere given my reasons for recognition of the Guatemalan and Chiapan population of *sacki* as distinct from the Oaxacan *bocourti* (Stuart, 1954 : 17-18).

In Guatemala this form has about the same distribution as *Sceloporus v. olloporus* except that it does not ascend to elevations above ca. 1100 m. Furthermore, the form does not extend southward beyond northwestern El Salvador (Mertens, 1952: 55).

In its local distribution *sacki* gives every indication of being much less tolerant than *Cnemidophorus deppi deppi*. It does not, for instance, invade rocky areas to the extent that does *deppi* nor does it enter shaded areas (e.g., riparian forests). Finally, *motaguae* does not descend from the Southeastern Highlands to the Pacific versant as does *deppi*. In many respects the *Sceloporus-Cnemidophorus* relationship in Guatemala might be expressed as *Sceloporus v. olloporus* is to *Cnemidophorus s. motaguae* as *Sceloporus squamosus* is to *Cnemidophorus d. deppi*.

Mabuya mabouya alliacea Cope

Esquipulas, Nos. 106854, 106859 (3); Jutiapa, Nos. 106855 (3), 106860; Mongoy, No. 106856; Santa Catarina, Nos. 106857-58.

This tolerant, widespread, Middle American species was far more abundant on the Southeastern Highlands than the few collected specimens would suggest. It was especially common in the numerous rock walls or fences that are a conspicuous feature of the region, but it was found in such varied habitats as forest mulch along streams and dry pine forests. No. 106860 was secured at an elevation of 1125 m., higher than I can recall ever before having seen the species in Guatemala.

Scincella cherriei cherriei (Cope)

Esquipulas, No. 106849.

The single specimen of this species that I was able to secure was associated with *Mabuya m. alliacea* and *Gymnophthalmus s. birdi* in a deep layer of dried leaves in an oak grove. Known from El Salvador (Mertens, 1952: 58), the species is probably generally distributed over the Southeastern Highlands.

Scincella incerta (Stuart)

San Lorenzo, No. 106853 (2).

As records of this species continue to accumulate, its geographic pattern begins to take form. It now appears that, though overlapping both *Scincella c. cherriei* and *S. assata assata* (Cope) at their upper limits (ca. 1300 m.), it is confined to higher levels. That the species is fairly tolerant is indicated by its occurrence in such diverse environments as cloud forest and oak-pine forests.

The above specimens were found beneath a decaying pine log on a dry, rocky hillside at 1650 m. elevation.

Kinosternon cruentatum cruentatum Duméril and Bibron

Esquipulas, No. 107116; Jutiapa, Nos. 107114-15; Laguna del Pino, USNM No. 123659.

This is another species that very probably ranges across the Southeastern Highlands at lower elevations. Turtles are reported to live in a small lake on the outskirts of Jalapa at about 1500 m. If true, they are undoubtedly of this species and represent the highest record of this form in Guatemala. The Jutiapa specimens were secured on the outskirts of the village from a quiet stream the waters of which were noticeably saline. The Esquipulas individual was taken from a rain pond in a pasture. Turtles, probably of this species, were reported at other localities at lower elevations.

Boa constrictor imperator Daudin

Mongoy, No. 106754.

This species is probably present only along the edges of the Southeastern Highlands at low elevations. The single specimen was secured at 600 m. elevation from a shallow cave in the lava on the north shore of Laguna de Atescatempa a few kilometers south of Mongoy. It is a female with the following characters of scutellation: labials, 19/20—22/23; maximum number of dorsals, 70; abdominals, 223; subcaudals, 49. It has a body length of 831 mm. and a tail length of 100 mm.

Storeria dekayi tropica Cope

Esquipulas, Nos. 106732-33.

Like several other species previously noted, this form, typically Caribbean, has reached a pass to the Pacific versant yet has failed to spread in that direction, even though known from elevations up to ca. 1500 m. in Alta Verapaz. Both of the above specimens were secured from beneath the mulch in a coffee grove bordered by the Río Atulapa at 880 m. elevation. An adult female, No. 106732, taken on March 8

TABLE III

Variations in the major morphological characters in *Storeria dekayi tropica*

Number	Sex	Labials	Oculars	Temporals
106732	♀	7/8 - 6	1/2	1 + 2
106733	J	7 - 6/7	1/2	1 + 2
		Dorsals	Abdominals	Subcaudals
106732	♀	17	134	45
106733	J	17	129	53

contained nine eggs in the body cavity. The other specimen, a juvenile, was collected on May 27 and could not have been more than a few days old. For scutellation characters, see Table III.

Thamnophis cyrtopsis fulvus (Bocourt)

Las Nubes, Nos. 100513-14; Soledad Grande, S-1347(skull), CNHM No. 68610.

Like several species noted previously, *Thamnophis* is represented on the Southeastern Highlands at only relatively high elevations and is one of the forms that spills over from the Southwestern Highlands. The species apparently reaches the limits of its range on Soledad Grande. This aquatic-margin form is most generally encountered along the small streams that either flow through upland meadows or tumble down the steep mountain slopes.

Significant characters of scutellation are given in Table IV.

Drymobius margaritiferus occidentalis Bocourt

Jutiapa, No. 106726, CNHM No. 68608.

The Michigan specimen of this riparian form was found in the forest bordering the Río Amayito not far west of Jutiapa at 950 m. elevation. Several other specimens of this species were observed in this same

TABLE IV

Variations in morphological characters in *Thamnophis cyrtopsis fulvus*

Number	Sex	Labials	Oculars	Temporals
CNHM 68610	♀	8 - 10	1/3	1 + 4
100514	♀	8 - 10	1/3	1+2/1+3
100513	♂	8/7 - 10	1/3	1 + 3
		Dorsals	Abdominals	Subcaudals
CNHM 68610	♀	19-17	135	64
100514	♀	19-17	145	62
100513	♂	19-17	147	70

TABLE V

Variations in morphological characters in *Drymobius margaritiferus occidentalis*

Number	Sex	Labials	Oculars	Temporals
106726	♀	9 - 10	1/2	2 + 2
CNHM 68608	♂	9 - 10	1/2	2 + 2
		Dorsals	Abdominals	Subcaudals
106726	♀	17-15	150	. . .
CNHM 68608	♂	17-15	149	124

general vicinity. It probably does not range much beyond the 1000 m. contour.

Scutellation characters are given in Table V.

Oxybelis aeneus aeneus (Wagler)

Mongoy, No. 106730.

The single specimen of this form, typical of subhumid areas at elevations below 1000 m., was secured from a patch of dense brushland at 575 m. On the basis of data presented by Bogert and Oliver (1945: 381-92) the specimen represents an almost typical intergrade between *aeneus* and *auratus*, but the Guatemalan population of this form as a unit appears to be closer to *aeneus*. A fuller discussion of this problem will be presented later.

The above specimen, a female, had recently eaten a small *Cnemidophorus d. deppi*. Its scutellation is as follows: labials, 9-10/11; oculars, 1/2; temporals, 1-2; dorsals, 17-15-13; abdominals, 180; subcaudals, 163; body length, 770 mm. (tail complete but broken); eye just longer than the internasals.

Ninia sebae sebae (Duméril, Bibron, and Duméril)

Esquipulas, No. 106692 (2).

This mulch-inhabiting species is apparently extremely rare on the Southeastern Highlands, where suitable habitats are few. The above two specimens were associated with *Storeria dekayi tropica* in the litter of a banana grove by the Río Atulapa at 880 m. elevation.

The adult male, with the exception of the black and yellow collars, is pure red without any dark markings dorsally; in the juvenile specimen the dark dorsal markings are reduced to tiny black spots along the vertebral scale row. Though such reduction in pattern is not unusual in this form, it is rather surprising that it should occur in the only two specimens collected at this one locality.

The major features of scutellation are given in Table VI.

TABLE VI

Variations in the major morphological characters of *Ninia sebae sebae*

Number	Sex	Labials	Oculars	Temporals
106692	J	7 - 7	0/2	1-2
106692	♂	7 - 7	0/2	1-2
		Dorsals	Abdominals	Subcaudals
106692	J	19	137	56
106692	♂	19	136	59

Leptodeira annulata polysticta Günther

Laguna de Ayarza, USNM 125340; San Lorenzo, No. 106220.

I secured a single specimen of this species in early February from a bromeliad on a tree overhanging a small, almost dry stream at 1640 m. elevation. In 1949 some linesmen showed me a specimen that they had killed several days before in a barranca on the Las Nubes block at 2200 m. No other reptile on the Southeastern Highlands has so extensive a vertical range as does this species.

The Michigan specimen is a female with 8 supralabials, oculars 3/2, temporals 1-2, 199 abdominals, 97 subcaudals, and dorsals 21-23-25-23-21-19-17-15. It has a body length of 521 mm. and a tail length of 184 mm.

Leptodeira rhombifera Günther

El Carnero, CNHM Nos. 68613-14, 69113; Esquipulas, Nos. 106715, 106716 (3); Jutiapa, Nos. 98104-5; Laguna de Ayarza, USNM Nos. 125341-48.

In a previous paper (Stuart, 1954: 18-19), I attempted to show that this species is probably related to *maculata* of southern Mexico and that the group has reached lower Central America via the Grijalva-Negro-Motagua corridor. This species may well be autochthonous to the southeast and its annectant uplands to the south.

On the Southeastern Highlands and indeed throughout all Guatemala *Leptodeira rhombifera* does not range above 1000 m. It seems to favor xeric regions as compared with *Leptodeira a. polysticta,* which is most frequently encountered in more mesic regions. With the onset of the rains the species is most generally to be found feeding on frogs at night in the vicinity of rain ponds.

The scutellation of the Michigan and Chicago specimens recorded above is given in Table VII.

Geophis rhodogaster (Cope)

Las Nubes, No. 100515; Santa Lucía, No. 106552.

This is another Southwestern Highland element that apparently

TABLE VII

Variations in morphological characters in *Leptodeira rhombifera*

Number	Sex	Labials	Oculars	Temporals
106715	J	8 - 9	1-2/2-?	1+3/1+2
106716	♀	8 - 10	1/2-?	1+3/1+2
106716	♀	8 - 10	2/2	1+2
106716	♀	8 - 10	2/2	1+2
CNHM 69113	♀	8 - 10	2/2	1+3/1+4
CNHM 68613	♂	8 - 10	2/2	1+3/1+2
CNHM 68614	J	8 - 10	2/2	1+2+2/1+2+3
		Dorsals	Abdominals	Subcaudals
106715	J	23-21-19-17-15	160	79
106716	♀	21-23-21-19-17	166	63
106716	♀	23-25-23-21-19-17	166	63 + tip
106716	♀	21-23-21-19-17	167	. . .
CNHM 69113	♀	21-23-21-19-17	165	79
CNHM 68613	♂	21-23-21-19-17	161	85
CNHM 68614	J	21-23-21-19-17-15	167	64

invades the Southeastern Highlands only in the higher elevations of their western section. Both of the above specimens were secured in the upper portions of the oak-pine belt (ca. 2000 m.). The Las Nubes specimen was found dead on a road and was partly mutilated and badly dessicated.

In both, the dorsals are smooth and disposed in 17 rows throughout the body length. In the perfect specimen there is no preocular, one postocular, and a single temporal. The Las Nubes specimen is a male with 131 abdominals and 40 subcaudals. The Santa Lucía individual is a female with 145 abdominals, but 31 subcaudals, a body length of 264 mm., and a tail length of 49 mm.

Stenorrhina feminvilli Duméril, Bibron, and Duméril

Jutiapa, S-1348 (skull); San Lorenzo, Nos. 106711-12.

No. 106712, an adult female, was found dead on a trail that formed a common boundary between a pine forest and a patch of scrubby oak second growth. The elevation of 1750 m. is, to my knowledge, the highest level at which this species has ever been collected. It was taken on February 15 and contained five fully developed eggs. No. 106711 is a juvenile from a somewhat lower elevation by a small stream that flowed through dense second growth. No. S-1348 is the skull of a specimen found dead along a trail through an oak grove near a small stream.

The dorsal body pattern of all three specimens consists of five dark stripes on a gray background. Features of scutellation are given in Table VIII.

TABLE VIII

Variations in the major morphological characters in *Stenorrhina freminvilli*

Number	Sex	Labials	Oculars	Temporals
106711	♀	7 - 7/8	1/2	1+2
106712	♀	7 - 7/8	1/2	1+3/2+3
		Dorsals	Abdominals	Subcaudals
106711	♀	17	167	35
106712	♀	17	175	35

Conophis pulcher pulcher Cope

Mongoy, No. 106725.

There is at present, in my opinion, considerable confusion in the trivial synonymy of the genus *Conophis*. This matter will be taken up in a future paper, and it is sufficient to note for the present that if the Pacific versant population of *Conophis pulcher* is different from the Caribbean population (which I seriously doubt) it must stand as *Conophis pulcher plagosus* Smith and not as *Conophis pulcher similis* Bocourt to which it has been assigned by Smith (1942: 395). At any rate the above specimen falls within the range of variation in pattern of a small series of specimens from the Motagua Valley and has a small dark punctation on the outer ends of some of the ventral scutes.

This form is apparently another example of continuity between Pacific and Caribbean populations via the Southeastern Highlands, though such continuity is probably tenuous and restricted to elevations below 1000 m. The specimen was found in a banana grove at 550 m. by Luis de la Torre. It is a female with the following scutellation: labials 8/10, oculars 1/2, temporals 2+2/2+3, dorsals 19-17, abdominals 171, tail incomplete.

Bothrops godmani (Günther)

Los Ocales, No. 106745, S-1038 (skull).

A head and tail and a head of this not uncommon highland viper was presented me by my friend Pat Odonnell, son of my host at Los Ocales. Both were secured at approximately 2000 m. from a mixed stand of pine and oak. The species probably does not descend much below this level. The more complete specimen proves to be a male with 9 supralabials, 11 infralabials, 1 preocular and 3 postoculars, and 30 subcaudals.

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PLATE I

FIG. 1. Northeastward across the Esquipulas Basin from above Esquipulas. Cultivation is restricted largely to the lower mountain slopes and the edges of the basin, where permanent streams supply water for irrigation. The impression of fairly extensive forested areas on the basin floor is produced by the repetition of low vegetation bordering the intermittent streams that cross the basin. March, 1952.

FIG. 2. Scrubby dry-land vegetation characteristic of the plains in the Mongoy region. Land of this type is utilized as pasture. Volcán Suchitán in the background. April, 1952.

PLATE I

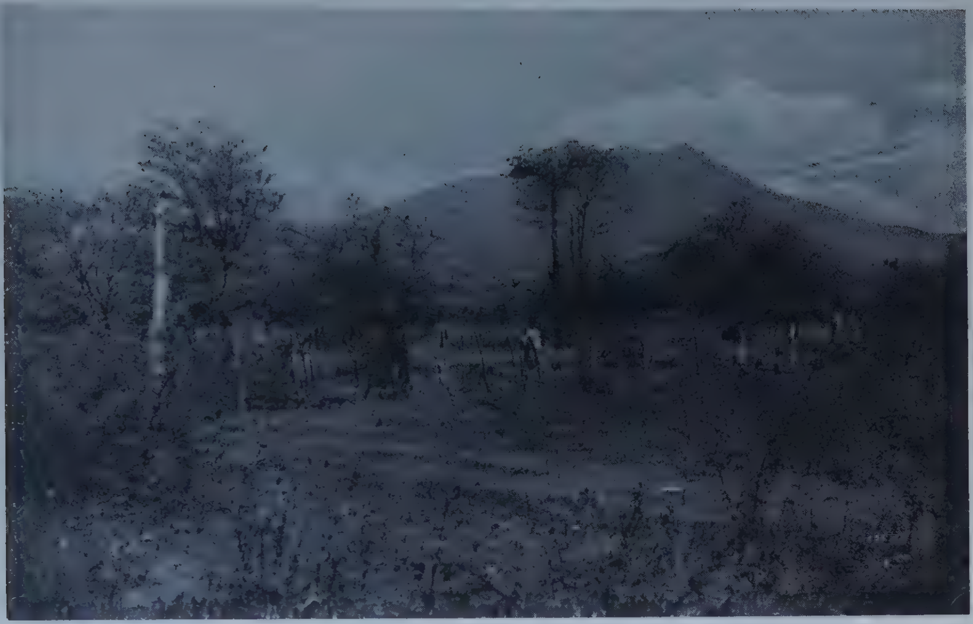

Fig. 1

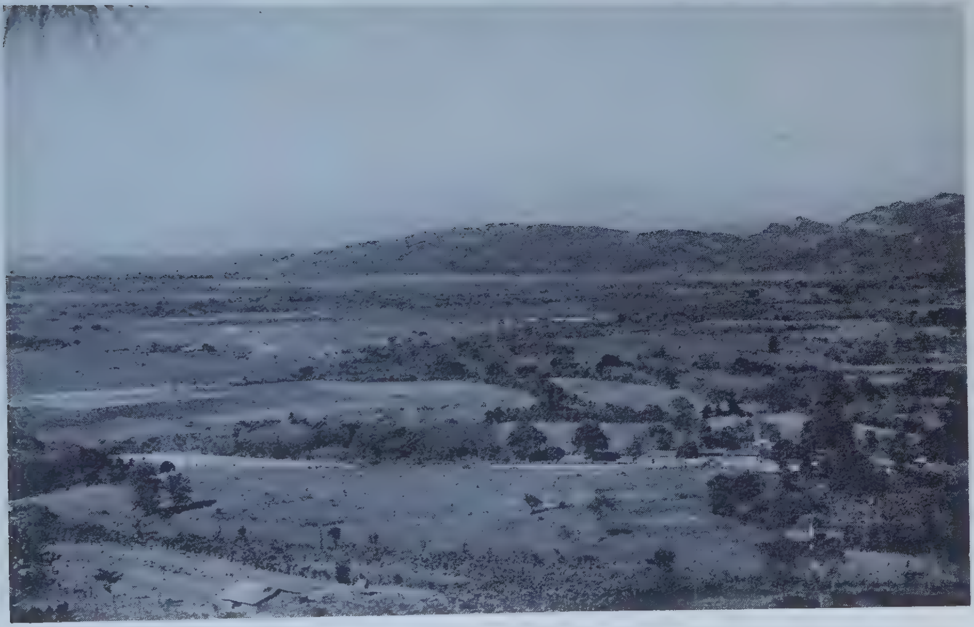

Fig. 2

PLATE II

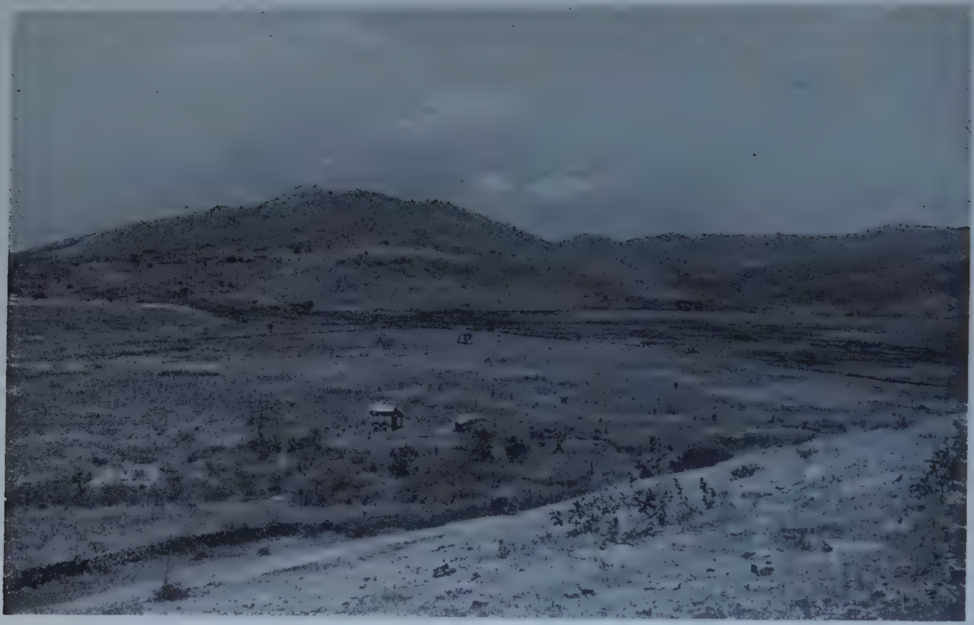

Fig. 1

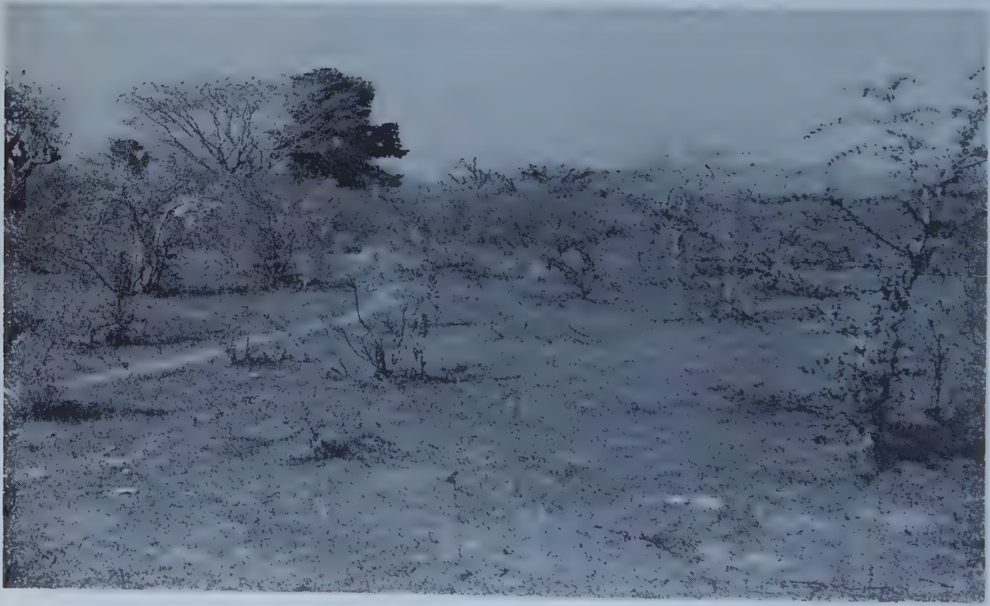

Fig. 2

PLATE II

FIG. 1. Westward across the plains to the more rugged terrain west of Jutiapa from a hill just west of the village. The plains in the foreground support a cover of tall grasses, and the hills in the background are almost barren with only a discontinuous grass cover such as is present in the immediate right foreground. The rock wall at the base of the slope in the foreground is especially typical of the Jutiapa region. March, 1952.

FIG. 2. Short-grass plains south of Jutiapa. The *mimosa* and *jicaro* that constitute the bulk of the larger plants often form an almost impenetrable thicket. This photograph was taken only a few minutes before fire swept through the area. March, 1952.

PLATE III

FIG. 1. An opening in the riparian forest along the headwaters of the Río Chimalapa just west of San Pedro Pinula. March, 1952.

FIG. 2. An oak-grove in the vicinity of San Lorenzo. The ground cover is short grass. All the oaks of this region support a heavy growth of Spanish moss. February, 1952.

PLATE III

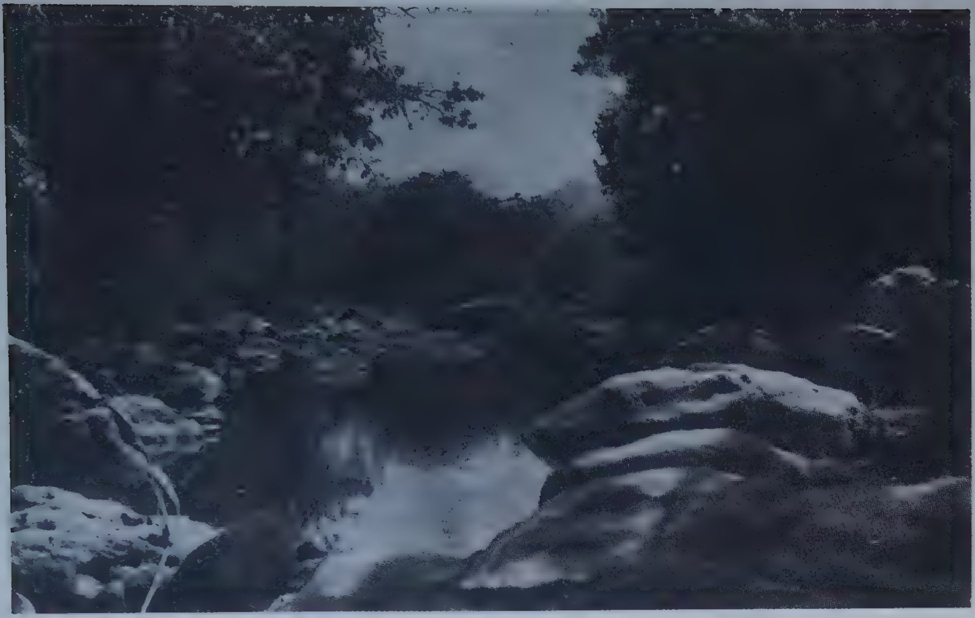

Fig. 1

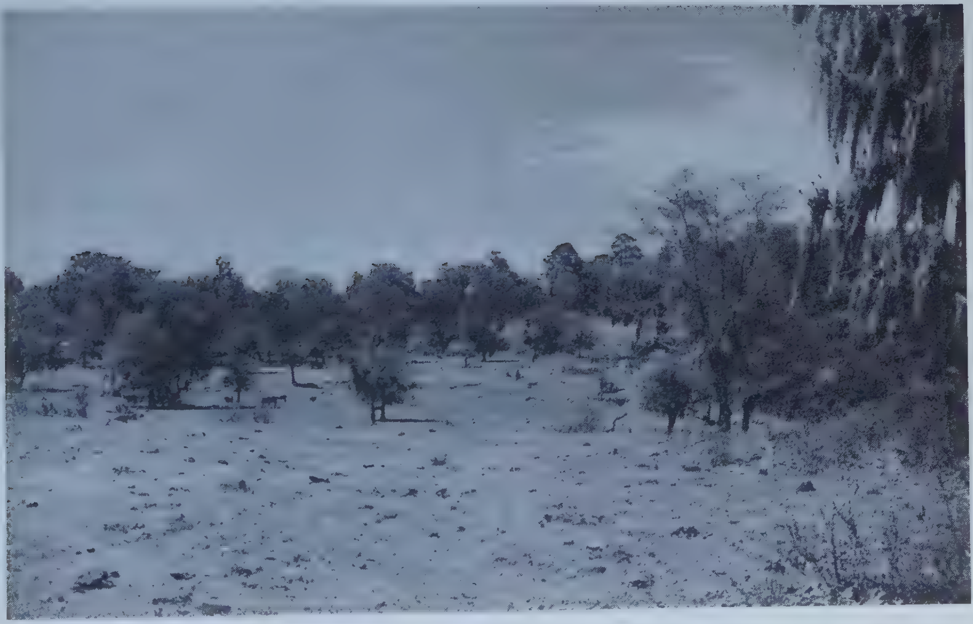

Fig. 2

PLATE IV

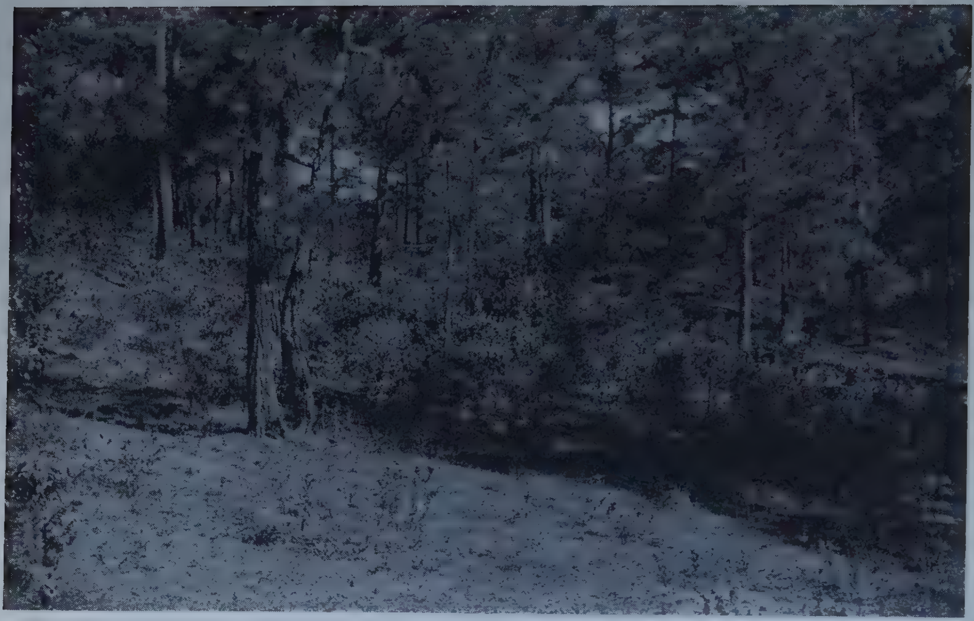

Fig. 1

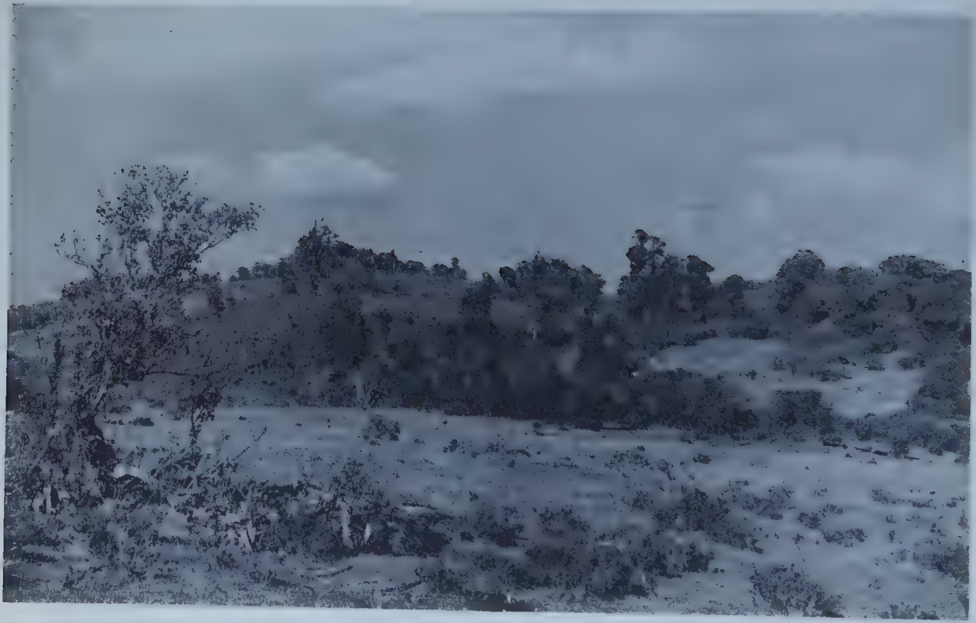

Fig. 2

PLATE IV

FIG. 1. A pine grove in the vicinity of Esquipulas. The forest floor, as in most pine groves in the southeast, supports a cover of short grasses and is remarkably free of undergrowth. March, 1952.

FIG. 2. The rolling high plains in the vicinity of Soledad Grande. The ground cover is short grass, small herbs, and lichens. There are also occasional thickets of shrubs such as appear in the depression in the mid-distance. Virgin broadleaf forest crowns the hill (the highest point on the Soledad Grande block) in the background. March, 1952.